The Ecological Functions of Asian Elephants in the Sundaic Rainforest: Herbivory and Seed Dispersal

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Abstract

Asian elephants (*Elephas maximus*) are among the last remaining megaherbivores in the Sundaic rainforests. In this thesis, I aimed to improve our understanding of the ecological roles of rainforest-dwelling Asian elephants through their herbivory and seed dispersal behaviours. A comprehensive review in Chapter One revealed that there have been few investigations of their interactions with the community and the habitats they live in. In Chapter Two, I advanced our understanding of Asian elephants in modifying the rainforest structure by quantifying their diet selection and herbivory impacts. The principal foods of Asian elephants in rainforests were palms (39% of total trunkfuls consumed) and trees (30%). They preferred monocots, particularly palms (preference ratio=4.6; below 1=avoidance) that are not abundant in the forest, and most monocots sustained high damage due to elephant foraging (above 40% in foraged patches). Their feeding behaviour was associated with a reduced palm density in the Royal Belum rainforest where elephants roam, as compared to a forest lacking elephants in Krau Wildlife Reserve. Although large tree saplings (around 2±1 cm diameter) were vulnerable to elephant damage, they had high recovery rates, and elephant herbivory is likely not the sole factor causing lower tree sapling density in Belum. Asian elephants are important seed dispersers. In Chapter Three, I recorded rare interactions of Asian elephants and a large-fruited rainforest tree, *Irvingia malayana* (Irvingiaceae) through the use of camera-traps. The removal rate of fruits by elephants was low, yet seed dispersal by elephants allowed *Irvingia malayana* seeds to escape from high levels of seed predation by wild boars. In Chapter Four, using network analysis, I identify Asian elephants as dominant functional generalists promoting seed dispersal diversity within the community. This is the first highly diverse seed dispersal network in the Sundaic region, built using an inter-disciplinary approach, which combines ethnobotany knowledge, feeding signs on fruits, camera-trapping, and published literature. Elephants had high species strength and were important to both the dispersal of plants central to the network and the dispersal of large-fruited species. Along with other important seed dispersers such as gibbons (the most efficient seed dispersers), binturong, civets, and the Malayan sun bear, they promoted network nestedness and functional redundancy. Simulation of defaunation of important, highly-connected seed dispersers caused adverse co-extinctions of seed dispersal interactions. Urgent protection of important and vulnerable rainforest species is needed in the Sundaic region. This thesis confirms the importance of Asian elephants as selective feeders for palms and tree saplings. It describes their interactions with tropical Sundaic fruits and confirms Asian elephants as functionally dominant seed dispersers within the seed dispersal community.

Acknowledgment

I was privileged to work in one of the world's most remarkable rainforest, the Belum Temenggor Forest Complex, to study the last remaining megaherbivores, the Asian elephants, and to extend the study to nature's web of life with the local indigenous people, the Orang Asli.

This research has received generous funding support from Yayasan Sime Darby (grant M0005.54.04), and the University of Nottingham Malaysia. I thank Puan Dr. Hajjah Yatela Zainal Abidin for the continuous support she and her team had provided to MEME. I thank the Department of Wildlife and National Parks (DWNP), the Perak State Parks Corporation, the Forestry Department of Perak, and the Department of Orang Asli Development (JAKOA) for the approval of permits. I am grateful to Nasharudding Osman and Mohamad Khairul Adha bin Mat Amin from the Kuala Gandah National Elephant Conservation Center (NECC), for making the elephant feeding observations possible in Krau Wildlife Reserve.

My supervisor, Prof. Ahimsa Campos-Arceiz provided this special opportunity and allowed me the freedom to explore my ideas. This thesis would have been impossible without his enthusiasm for seed dispersal and megafauna, and faith in his Ph.D. student. The dynamics he created for his lab, the Management and Ecology of Malaysian Elephants, MEME, has introduced diversity (people and science) into my research environment. My co-supervisor, Dr. Kim McConkey has inspired me with her unrelenting patience for young researchers and obsession with nature. She has stimulated my thinking in the forests and strengthened my knowledge in natural history and seed dispersal science. I am incalculably grateful for both of their rich contributions and the time they spent reviewing the long bouts of writing before this final thesis.

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words that a Ph.D. student's responsibility is to produce good science. Both examiners had provided valuable advice for my progress. Equally important to the successful completion of this thesis, was the constructive and positive feedback provided by both internal (Chris Gibbins) and external examiners. I have benefitted from the penetrating mind and experience of Dr. Luis Santamaria during the viva.

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Statement of Contribution

I conceived the main research questions, develop and refined methods, execute preliminary tests and the main research, carried out all fieldwork and ensured that the collected data was of good quality to answer the research questions, processed collected fruits, created herbariums to distinguish morpho species, consolidated plant lists and identified collected plant species, created a plant and seeds catalogue for LEK interview, led LEK interviews, led literature reviews, processed and cleaned data, brainstormed analyses, produced all figures and tables and led all writing in this thesis.

My supervisor Campos-Arceiz A and co-supervisor McConkey K helped with the formulation of ideas, contributed feedback on analysis, results, and discussion for all chapters in the thesis. They also reviewed and revised the manuscripts several times before we finalized the final manuscripts. Campos-Arceiz A joined field trips for Chapter Two, and McConkey K joined field trips for Chapter Three and Four and provided valuable suggestions for the methods applied. All field trips from Chapter Two to Four were assisted by our local indigenous field assistants, permanent staffs of MEME — Param P, Ridzuan A, Cherang TMT, and Husin S. They contributed greatly to the LEK knowledge for Chapter Four.

At the early stage of the Ph.D., I had experimented with different techniques, collected data from both the Royal Belum State Park (RBSP) and Temengor forest reserve (TFR) in the Belum Temengor Forest Complex (BTFC), and refined methods to understand the system. Although most data from this stage was not included in the main chapters, Loo YY assisted as a research assistant for six months, and I received support from Solana-Mena A and our field assistants, including Khairil O (ex-MEME field assistant), who introduced me to the forests around BTFC and attempted to track collared elephants for measuring herbivory.

Chapter One was written to provide an overall understanding of the ecological functions of elephants and to identify the knowledge gaps concerning the Asian elephants in the Sundaic rainforest. Bechtold T and Sanjay R helped proof-read the final manuscript.

The following chapters in this thesis are intended for submission for publications:

Chapter Two is prepared for submission as Ong L, Terborgh J, Davenport LC, Tan WH, Stephane AM, Param P, Rizuan A, Nasharudding O, Mohamad KAMA, and Campos-Arceiz (2020) Diet selection and herbivory impacts of Asian elephants in Peninsular Malaysia. Terborgh J, Davenport LC, and Campos-Arceiz A helped conceived ideas and reviewed the manuscript. Mohamad KAMA from the Kuala Gandah National Elephant Conservation Center

(NECC) made arrangements for his team of mahouts — Ali G, Fadhlul HAS, Khairul A, Muhammad I, Lukman M, Syed NA, Sulaiman M, Rizuan M, and Mohamad SA to guide the elephants to the feeding sites. Co-authors and the field team, including Loke PW, Loo JS, Hii N, and Solana-Mena assisted with elephant feeding observations and data entry. Meredith M provided some feedback for data analysis. Tan WH also assisted with logistic arrangements and commented on the final manuscript.

Chapter Three is published as Ong L, McConkey K, Solana-Mena A, and 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 Bulletin of Zoology, 67: 1-11. Solana-Mena A assisted with logistics arrangements and Lee ZY assisted with fieldwork. Wadey J provided feedback for the final manuscript.

Chapter Four is intended for submission as a method and a results paper.

Methods paper:
Ong L, Campos-Arceiz A, Nurul AA, Ong L, Loke PW, Param P, Cherang MTT, Husin S, Rizuan A and McConkey K (2020) A multi-disciplinary approach and the use of local ecological knowledge to build a highly diverse seed dispersal network.

Results paper:
Ong L, McConkey K, Nurul AA, Ong L, and Campos-Arceiz A (2020) The seed dispersal network of Royal Belum, a megafauna-rich tropical rainforest.

Nurul AA assisted with LEK surveys and acted as the main translator. Solana-Mena A, Param P, and Cherang MTT helped contact participants and also assisted as translators for some surveys. Nurul AA and Ong L contributed to the literature search and data entry. Loke VPW and Praveena C provided feedback for the final manuscript. The participants whom we interviewed and contributed to the LEK from Kg. Tiang were Roy H, Ismail J, Mamak P, and Hasan P. Participants from Kg. Semerloh, were Ismail A, Eim J, Hamid P, Apok A, Jaafar A, and Abain G. Participants from Kg. Sungai Kijar were Tok Batin Radi L, Lanas T, Jali R, Rajut T, and Hamid K. Participants from Kg. Pulau Tijuh were Hasim C, Ajim A, Sham H, and Long bin T. Participants from Kg. Desa Damai were Beracut L, Arrifyn D, Deney A, and Johar B. Participants from Kg. Banun were Selerwer N, Dalong P, Selan M, and Saken U.

Chapter Five surmised and discussed the key findings of the thesis, provided suggestions for future studies, as well as implications related to the research. Oi Ching and Loke VPW provided feedback for the final manuscript.

The following papers are not included in this thesis but are intended for submission:

Ong L, McConkey K, Loke PW, Loo YY, Tan WH, Husin S, Cherang MTT, Param P, Rizuan A, Solana-Mena A and Campos-Arceiz A (2020) Fruiting Phenology and Food Availability for the Belum Tropical Rainforest Community.

Ong L, McConkey K, and Campos-Arceiz A (2020) Keystone plant resources and functional fruits of the frugivory network of the Belum tropical rainforest.

Ong L, McConkey K, Loo YY, Hii YM, Hii N, and Campos-Arceiz A (2021) Fruit traits and seed dispersers of the Belum rainforest, Peninsular Malaysia.

The phenology data were collected monthly (approximately 5 days field trip) from August 2016 to November 2017. Loke PW assisted as a research assistant for the full study period. Tan WH assisted as a research assistant from March to Nov 2017. During this period, Tan WH also helped distinguish the Fagaceae species and explored plant identification (ID) with DNA barcoding techniques. We did not follow up with this application due to time constraints and a limited budget. During the fruiting peak periods, McConkey K joined the field trips and Solana-Mena A assisted with logistics and data collection. Lim TW provided a list of plants from Perak (referenced Turner 1995), Loke PW, Nurul AA, and Hii YM helped with the collection of the pictorial library for plant ID.

I co-authored the following paper:

John Terborgh, Lisa C. Davenport, Lisa Ong, and Ahimsa Campos-Arceiz (2017) Foraging impacts of Asian megafauna on tropical rain forest structure and biodiversity. Biotropica. 0(0): 1-6. Tan SL produced the map for the manuscript.

Conferences attended:

International Science and Nature Congress (ISNAC) 2015, participant

Society of Conservation Biology (SCB) 2016, poster and speed talk presenter: Elephant frugivory and wild boar seed predation of *Irvingia malayana*, a large-fruited tree, in a rainforest of Peninsular Malaysia.

VII International Frugivores & Seed Dispersal Conference, 2020, speaker of "Two sides of the coin: defaunation and rewilding effects on frugivory and seed dispersal" symposium: The seed dispersal network of Royal Belum, a megafauna-rich tropical rainforest.

Workshops and events attended:

Biodiversity Conservation Society Sarawak (BCSS): Boot camp in wildlife study design and data analysis (10 days), and Introduction to GIS with QGIS and R (6 days).

SCB 2016, Linear Modelling (6 days)

Forest Research Institute of Malaysia (FRIM): Tree Identification Course

Produced materials and joined several MEME outreach programs to promote elephant conservation.

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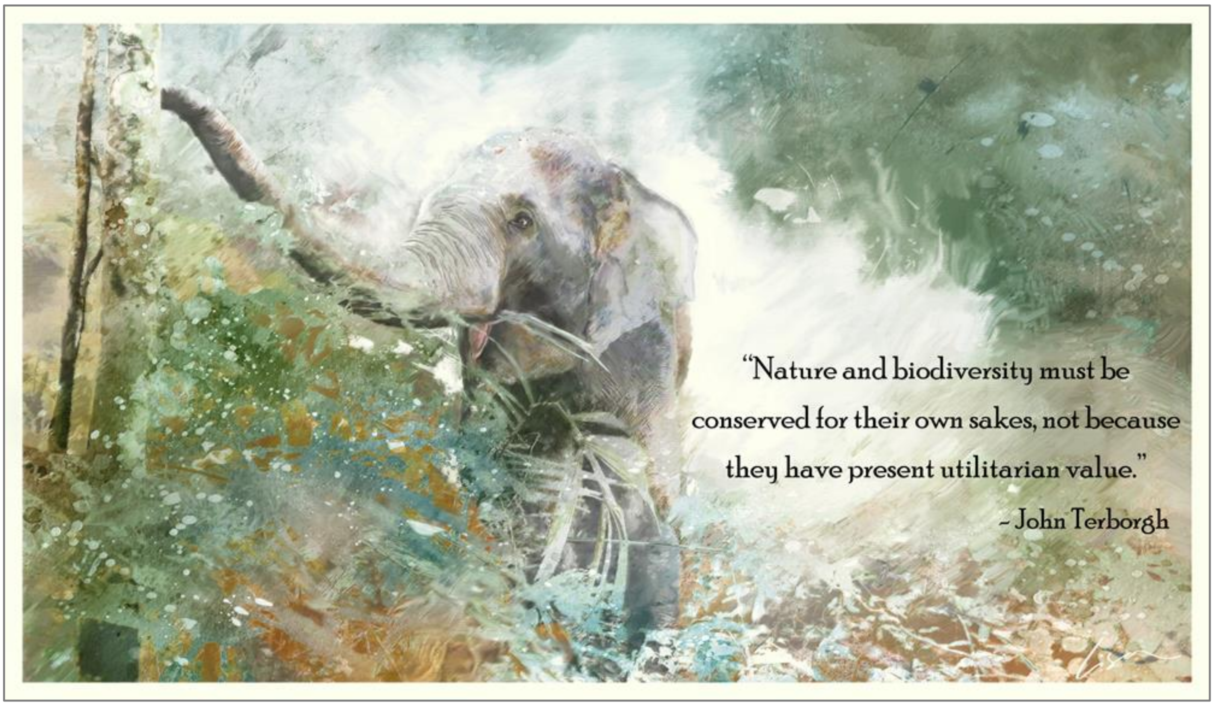


"Nature and biodiversity must be conserved for their own sakes, not because they have present utilitarian value."

~ John Terborgh

CHAPTER ONE

Introduction:
Ecological Function of Elephants,
Trophic Interactions and Mutualistic networks

Elephants are widely known as effective long-distance seed dispersers (e.g., Babweteeraa et al., 2007; Campos-Arceiz et al., 2008a; Blake et al., 2009; Bunney et al., 2017) and ecosystem engineers – organisms capable of modifying or maintaining habitats as they modulate the availability of resources of other species (Lawton & Jones, 1995; Jones et al., 1994; Haynes 2012). Despite this recognition, most studies defining the ecological influence of elephants have been based on the savannah and woodland habitats of African elephants (*Loxodonta africana* and *Loxodonta cyclotis*) (Buechner & Dawkins, 1961; Dublin et al., 1990; Asner & Levick, 2012). Studies of Asian elephants (*Elephas maximus*) relate more commonly to food habits and resource utilization (e.g., Olivier, 1978; Baskaran, 1998; Ahrestani et al., 2012; English, 2014a). Their effects on habitat modification remain poorly understood (e.g., Mueller-Dombois, 1972; Ishwaran 1983).

The ecological influence of Asian elephants is best represented by their seed dispersal ability (Campos-Arceiz et al., 2008a; Campos-Arceiz & Blake, 2011; Sekar, 2016). The diversity and number of seeds dispersed by Asian elephants in tropical rainforest appear to be considerably lower (e.g., Kitamura et al., 2002; Kitamura et al., 2007 in Thailand; Campos-Arceiz et al., 2008 in Myanmar; Varma et al., 2008 in Vietnam), than African elephants in African landscapes (Gautier-Hion et al., 1985; Blake et al., 2009; Babweteeraa et al., 2007) and Asian elephants in seasonal forests (e.g., Sri Lanka; Samansiri & Weerakoon, 2007).

"The activities of large African mammals reverberate through their ecosystems" (McNaughton at al., 1988). Large mammals are highly interactive animals with ecological niches that affect ecosystem processes. Our understanding of the functional role of Asian elephants in structuring their environment remains poorly understood (Dudley,1993). The Asian elephant may be extinct before comprehensive studies of its role in tropical forest ecosystems of Southeast Asia can be assessed.

To understand the ecological functions of Asian elephants, I present a comprehensive review within this chapter of the key themes across my Ph.D. ***This chapter*** **first introduces elephants as megafauna and their ecological significance as ecosystem engineers and seed dispersers**. The influences of elephants foraging on landscapes are drawn mostly from African studies, as studies on Asian elephants have not been done on a similar scale. The inclusion of studies on African elephants allows us to have a broader picture of how elephants interact with different ecosystems. When available, I have provided **examples of herbivory related studies on Asian elephants**. Most Asian elephant studies are predominantly diet oriented, with little information relevant to the impacts of browsing on stems and forest structure, especially in closed canopy rainforests. As part of this thesis aims to determine the seed dispersal relationships of Asian elephants with the rest of the entire community, **the seed dispersal function is explained from a mutualistic network approach**; **it is supported with reviews on seed dispersal interactions and strategies of the vertebrate communities**. The final section introduces **concepts of network structure**.

ASIAN ELEPHANT, THE MEGAHERBIVORE

Elephants, including the African bush elephant, the African forest elephant, and the Asian elephant, are amongst the few terrestrial megafauna (animals not less than 44.4 kg or 100 lbs; Martin, 1984), and mammalian megaherbivore (animals with a body mass of at least 1000 kg; Owen-Smith, 1992) still existing today. Consisting of the subspecies *Elephas maximus indicus* from the Asian mainland, *Elephas maximum borneensis* from Borneo, *Elephas maximum maximus* in Sri Lanka, and *Elephas maximus sumatrensis* in Sumatra, the Asian elephant is the only descendant of the proboscidean, family Elephantidae left on the Asian continent. (Fleischer et al., 2001; Sukumar, 2003).

Asian elephants are believed to have evolved from *Elephas hysudricus* during the Pliocene Epoch at around 5 to 6 million years ago (mya); their closest relatives include the extinct species *Elephas recki*, *Elephas antiquus*, and the dwarf elephants Elephas *falconeri* and *Elephas cypriotes*, all belonging to the Elephantidae family. *Primelephas,* the 'first elephant' from the late Miocene (11.6 to 5.3 mya in Africa, was ancestral to both *Loxodonta* and *Elephas*, as well as the mammoths *(Mammuthus).* Proboscideans originated in the late Paleocene Epoch around 60 mya with more than 160 recognised species. Other extinct families of Proboscidea include the Mammutidae, Gomphotheriidae, Stegodontidae, Deinotheriidae, and Palaeomastodontidae (Fleischer et al., 2001; Sukumar, 2003).

From the Pliocene to Pleistocene (around 2.6 mya to 11,700 years ago), megaherbivores spanned across various ecosystems, from open grasslands to deciduous woodlands, from tropical forests to savannahs. It was common to have two to six megaherbivores living alongside each other along with regional fauna. These megaherbivores included species from the Proboscideans, Diprotodontidae , Marsupiala, the Megatheriidae, and Mylodontidae in the Edentta, the Toxodontidae in the Notoungulata, the Anthracotheriidae, Hippopotamidae, Giraffidae, and the Artiodactyla. Between the late Pleistocene and Holocene, about 11,000 years ago, the diversity of megafauna dramatically declined (Owen-Smith, 1992). Their extinction globally is linked to both climatic and hominin drivers. Hominins have been interacting with megaherbivores since the migration of *Homo erectus* and contemporary hominins into Southern Asia and South and Western Europe, to the expansion of *Homo neanderthalensis* and the Denisovan humans into most of Eurasia and the eventual spread of modern humans (*Homo sapiens*) (Guthrie, 1984; Finlayson, 2005; Goebel et al., 2008; Lorenzen et al., 2011, Sandom et al., 2014).

Formerly distributed throughout most of tropical Asia, from West Asia along the Iranian coast into the Indian subcontinent and Southeast Asia, to as far north as the Yangtze River in China, the range of Asian elephants have shrunk from over 9 million km^2 to less than 500,000 km^2 at present (Olivier, 1978; Sukumar, 2003). There are now approximately 38,500–52,000 individual Asian elephants distributed in remnant populations found in India, Sri Lanka, Southern China, Thailand, Myanmar, Malaysia, and Indonesia (Sukumar, 2006).

In Malaysia, an estimated 2351–3066 wild individuals are left, with around 1251–1466 elephants in Peninsular Malaysia and 1100–1600 in Sabah (Sukumar, 2006). Elephants inhabit seven out of eleven states of Peninsular Malaysia, including major states such as Perak, Kelantan, Terengganu, Pahang, and Johor. Taman Negara National Park, covering 4343 km^2, holds the largest population of an estimated 290–631 elephants. Many large-bodied mammals, including Asian elephants, are affected by the loss and fragmentation of native forests (WCS, 2008; Saaban et al., 2011). As of 2010, Asian elephants are protected as an endangered species under the International Union for Conservation of Nature red list (IUCN). Nevertheless, we are far from understanding their ecological roles and have yet to explore the effects of their loss on ecosystems.

ELEPHANTS AS IMPORTANT MODIFIERS OF ECOSYSTEM DYNAMICS

African Bush Elephants as Ecosystem Engineers

Several authors have discussed the importance of large-bodied animals and megaherbivores on ecosystem dynamics and community interactions – including the influence of large herbivores or megaherbivores on individual plants, species composition, plant community structure, and habitat physiognomy (Owen-Smith,1988; Hester et al., 2006). These studies show how elephants indirectly modify below-ground processes and nutrient cycles (Hester et al., 2006; Pastor et al., 2006), and affect seed dispersal, seed predation, and recruitment processes (Bodmer & Ward, 2006; Gill, 2006; Terborgh et al., 2015). They also highlight the impact elephants can have on other fauna through ecological processes such as direct competition for food or indirect effects of habitat change (Suominen & Danell, 2006).

The overall influence of elephants is well illustrated in several African ecosystems where the relationship of large herbivores and plants is strongly connected (e.g., Cumming, 1982; Owen-Smith, 1989; Malhi et al., 2015; Terborgh et al., 2015; Ripple et al., 2016). The impacts of herbivores browsing and grazing affect plant physiology; generating regrowth flushes that enhance leaf production two to threefold (Teague, 1985). As leaf nutrient concentration and specific root uptake of nutrients increases, the growth rates of plants increase. Animal-mediated defoliation thus provides quality forage to other herbivores, creating a positive feedback loop for nutrient availability in the system (Ruess, 1984; McNaughton & Chapin, 1985).

In the savannahs, primary production is often limited by nutrients, rather than by water. As major consumers of resources, large mammals markedly stimulate and improve physiochemical processes associated with these nutritionally stressed systems. Plants digested and defecated contribute an additional gradient to the precipitation and mineralization pathway. This structural complexity, in turn, affects the regulation of energy flow, subsequently boosting primary productivity and speeding the turnover rates of land (McNaughton et al., 1988; McNaughton et al., 1997).

Large animals have strong organisational impacts on ecosystem processes and structures. Feeding by browsers, such as giraffes (*Giraffa camelopardalis*), mixed feeders such as the African bush elephants, and pure grazers such as wildebeests (*Connochaetes taurinus*) create partitioning of food resources that regulates habitats and the spatiotemporal distribution of food quantity. This creates pastures for other species and facilitates the seasonal movements of herbivores (McNaughton et al., 1988; Western, 1989).

A similar phenomenon occurs in the floodplains of Lake Rukwa, where African bush elephants and other large mammals open marshes to smaller-bodied ungulates (Vesey-Fitzgerald, 1960). In Amboseli, they open swamp and swamp pastures to other herbivores, trampling sedges which are replaced by higher quality grasses (Western, 1989). In the process of feeding on tree canopies, the African bush elephants create refuges for understory plants, preventing feeding by other large herbivores (Coverdale et al., 2016).

African bush elephants are major agents of habitat change. In the absence of cutting, elephants, and fires, grasslands could convert to dense bushlands (Western, 1989). In the Hluhluwe Game Reserve in South Africa, the extermination of elephants saw a reduction in the number of grazers and an increase in the population of browsers as a result of the thickening of the vegetation (Owen Smith, 1989). Within national parks, an artificially high density of African bush elephants feeding on shrubs and trees can eventually lead to a landscape of flattened vegetation, where trees disappear over hundreds of square kilometres (Sukumar, 2003). Termed the 'elephant problem' in the sixties, dramatic changes in vegetation cover had occurred in several woodlands and bushlands of Africa, including the Murchison (Kabalega) Falls National Park (Beuchner et al., 1963), Queen Elizabeth (Rwenzori) National Park in Uganda (Field, 1971), the Serengeti National Park (Lamprey et al., 1967), Tsavo National Park (Glover, 1963), and Ruaha National Park in Tanzania (Barnes, 1983). Trees such as the baobab *(Adansonia digitata)*, acacia (*Acacia albida*), and *Terminalia glaucescens* suffered high mortality from elephant browsing effects, with added pressure from drought and borer beetle attack (Laws, 1970a; Laws 1970b).

Woody plants in most ecosystems can tolerate elephant browsing due to their resprouting ability. In tree saplings, this ability aids survival, especially on frequently-burnt Savannahs. In adults, it enables plants to persist after disturbance from fire, flooding, or windstorms (Bond & Midgley, 2001). As compared to temperate forests (35.9%), tropical forests (51.5%) have a higher percentage of plants with the resprouting ability (Everham & Brokaw, 1996). Where logging and fires prevail, recovery by sprouting is also higher than in habitats where logging and fire were absent. Non-coppicing species such as the baobab thus suffer great mortality from heavy browsing by elephants (Bond & Midgley, 2001). Although plants are resilient, elephant browsing can still be detrimental in some habitats. In the Serengeti-Mara savannah, high elephant density, man-induced fires, and wildebeest trampling had inhibited regeneration, reducing the woodland to a grassland state (Dublin et al., 1990).

Tropical Africa is referred to as the "odd man out" for its comparatively depauperate alpha diversity as a tropical green forest (Gentry, 1988). Much of it is explained with historical, long, and short-term environmental variation, and differences in edaphic conditions (Parmentier et al., 2007). In Gabon, central Africa, Terborgh et al. (2015; 2016) found distinctly fewer small trees (<20cm dbh) and lower diversity in saplings than canopy trees as compared to Amazonian forests. Where there is a higher density of elephants, the density of small saplings and diversity of large saplings is also lower. By extensively damaging tree saplings (ground level: 71%, slopes: 43%), African forest elephants act as powerful filters on the tree recruitment process.

The Diet of Proboscideans and Elephants

The impact of elephants on vegetation is mostly a result of their metabolic needs, feeding, and ranging behavior. With their huge body mass, a group of ten elephants can consume 1,800 kg of vegetation per square kilometre each day and a further 1,200kg can be destroyed in the process (Sukumar, 2003). The crown height of mammalian cheek teeth, or level of hypsodonty, is commonly used to differentiate their feeding behavior (Janis, 1988). Hypsodonts have high tooth crowns and are prominent in mixed feeders and grazers who feed in more open, less forested habitats. Brachydonts are browsers with low tooth crowns that are unable to withstand high wear rates from grazing. The adaptation to a mixed browser diet is reflected both in the crown height and molar morphology of elephants. Elephants have high-crowned elephantid check teeth, indicating some degree of grazing in their dietary habits (Janis et al., 2004). Additionally, they have ‘multilophed’ parallel ridges of enamel like rodents and wombats (Janis, 1998; Janis et al.,2004). This morphology is different from what is found in specialised ruminants and perissodactyls that possess complex ‘plagiolophodont’ with cross-linked occlusal enamel surfaces (Janis, 1998; Janis et al.,2004).

In fossil studies, the $\delta_{13}C$ on tooth enamel is commonly used to assess the diet of herbivores. The presence of stable $\delta_{13}C$ of carbonate from fossil enamel provides indications of the $\delta_{13}C$ of the dominant type of food consumed by the herbivores (Cerling et al., 1999; Puspaningrum et al., 2014). Isotope records of modern and fossil proboscideans indicate C_3 browse as the main diet of both *Loxondonta* in Africa and *Elephas* in Asia. In some elephants, however, C_4 grass is essential to their diet (Cerling et al., 1999). C_3 plants are mostly plants such as trees and shrubs that use the C_3 photosynthetic pathway (or Calvin cycle) as compared to plants such as tropical and subtropical warm grasses and sedges that use the C_4 photosynthetic pathway for carbon fixation. Except for bamboos from higher elevations, C_4 plants can also be found in East, Central, and South Africa, as well as the central and eastern regions of southern North America. Bamboos, as well as grasses and sedges in Mediterranean and cool climates, are C_3 plants sharing the same isotope signal as C_3 browse. Proboscideans from western Europe and northern Eurasia thus had strict C_3 diets (Bocherens et al., 1994; Cerling et al., 1999). The differences between C_3 and C_4 pathways used by grasses can confound stable isotope studies, especially when comparisons are made between cool and warm climate habitats.

The straight-tusked elephant (*Palaeoloxodon antiquus*), a close relative of the Asian elephant, roamed Eurasia from the early Eopleistocene to the late Pleistocene (781,000–50,000 years before present, BP). It was forest-dwelling, being able to both graze and browse (Palombo et al., 2005). Most proboscideans in Africa and Southern Asia had a C_4 dominated diet from around 7 Ma up until their subsequent extinction. For *Elephas* in Asia, and both *Loxodonta* and *Elephas* in Africa, C_4 vegetation had been the dominant diet between 5–1 Ma (Cerling et al., 1999). Stegodons, from the subfamily Stegodontinae under Proboscidea, were present from 11.6 mya to the late Pleistocene (Pleistocene: spanning approximately 2.6 mya to 11,700 years ago). Stegodons lived across large parts of Asia and East and Central Africa and in Wallacea, such as Flores, that were never connected to the Asian continent. Two successive Stegodon species, *S. sondaari,* and *S. florensis* existed in Flores. *S. sondaari* was found to be a mixed feeder, while *S. florensis* had a predominantly C_4 diet (Puspaningrum et al., 2014).

In Northwest China, the East Asian summer monsoon has been suggested to create a shift in both climate and diet patterns. Along with all other mammals such as horses (Family Equidae), rhinoceros, bovids, deer, giraffes, and pigs, evidence from fossil teeth revealed that Asian elephants from the Linxia Basin in China lived in habitats where C_3 vegetation dominated in the late Cenozoic (before 2–3 Ma). C_4 grasses only expanded in the Quaternary (2 – 3 Ma till present). During this period, the diets of horses and bovids ranged from a pure C_3 to a mixed C_3/C_4 diet, with C_4 plants making up as much as 60% of the diet. C_4 grasses only became part of the diets of horses and bovids with increased seasonality (Biasatti et al., 2010).

At present, elephants are mixed feeders whose dietary behavior varies with habitat type, season, and different geographic range (Barnes, 1982; McKay 1973; Tchamba & Seme, 1993; Chen et al., 2006; Steinheim et al., 2005; English, 2014a). Plant families important to elephants in both continents include the Poaceae (the grass family), Cyperaceae (the sedge family), Arecaceae (the palm family), Fabaceae (the legume family), Euphorbiaceae (the spurge family), Combretum (the combretum family), Rhamnaceae (the buckthorn family), Anacardiaceae (the cashew family), Moraceae (the mulberry family, including figs), Malvaceae (the mallow family), Sterculiaceae (the sterculia family), and Tiliaceae (the basswood family) (Sukumar, 2003). Although a mixed feeder, browse likely dominates the diet of Savannah elephants more than graze as indicated by the isotope surveys (Cerling et al., 1999). In Asian elephants, there is no strong evidence to determine if they are more strongly browsing or grazing. Thus, referring to them as 'mixed feeders' is appropriate. Between African and Asian elephants, tooth morphology suggests that African elephants are more dominant browsers than Asian elephants.

Herbivory Influence of Asian Elephants

In comparison to their African counterparts, browsing by Asian elephants appear less destructive. In the semi-deciduous forests, savannas, and grasslands of Gal Oya, Sri Lanka, Ishwaran (1983) found that branch breaking, main-stem breaking, and stem twisting made up 78% of damaged woody plants. Bark peeling ranged between 12–25% and less than 15% of trees were pushed over. This distribution of herbivory impact would likely allow most plants to resprout and survive from direct damage. In the Ruhuna National Park, Mueller-Dombois (1972) found crown distortions concentrate on woody plants 2–5m tall, with higher damage (50–80%) in some species than others (25–50%). Elephants foraged in areas of high vegetation diversity with open grass cover during wet seasons and in closed woody vegetation during dry seasons. The habitat was able to withstand browsing throughout the drought season.

The African bush elephants have important effects on landscapes, ecosystems, and biogeochemical cycles. Although African forest and Asian elephants also impact tree stems in several landscapes, the constraints of field-based studies and limited durations have made it difficult to understand their roles at the same level as African bush elephants, especially in tropical ecosystems. We have little information relevant to the effects that Asian elephants have on vegetation in the Sundaic forests, particularly in Peninsular Malaysia.

Herbivory Influence of Asian Elephants in Sundaic Forests

Unlike on the savannahs, trees from the *Dipterocarpaceae* family dominate 50–80% of Malaysian rainforest canopies (Appanah, 1985). Leaves and bark of trees have high concentrations of phenolic compounds such as tannins that help plants defend against herbivores. Latexes and resins are physical irritants that are potentially toxic to herbivores. Mature leaves are high in fibre and protein, unpalatable to most herbivores (Turner, 2004). Arboreal folivores such as leaf monkeys have an advantage in harvesting young leaves from subcanopy trees and have evolved gastrointestinal modifications that can accommodate bacteria to help with the digestion of cellulose and hemicellulose tissues, as well as to detoxify secondary compounds (Chivers & Hladik, 1980). Where light is limited in the understory, resources available to animals are constrained. In such an ecosystem, how do Asian elephants harvest food and will they have assumed a significant role in altering the structure or composition of a mature rainforest? Will rainforest Asian elephants contribute to any large-scale elephant-mediated cascading effects that could define them as ecosystem engineers?

Olivier (1978) first encountered riparian vegetations that appeared to be maintained by animals, in particular, elephant activity. He speculated that Asian elephants also retard natural regeneration as African bush elephants did by trampling, ringbarking, pushing over trees, or pulling down lianas. Over his study period, however, he observed few trees pushed over by elephants and saw no signs of bark feeding in the rainforest of Peninsular Malaysia. Similar to African elephants, Asian elephants appeared to be selectively feeding on smaller size classes of trees. Olivier believed that Asian elephants do not contribute to the physiognomy of mature forests or the creation of secondary habitats in the rainforest, but may over the long term, affect the composition of mature stands with selective feeding.

Asian elephants may play a small but significant role in maintaining secondary habitats created by other means. In Sumatra, for example, Rappard (*unpublished* 1977; cited in Olivier 1978) referred to elephants as stabilisers of bamboo habitats, paraclimax vegetation, created by volcanic disturbance. Rappard once found evidence of bark feeding but never from big standing canopy trees. In the functional context, the extent to which Asian elephants destroy stands and the role they play in the maintenance of secondary habitats still has little evidential support, and speculations were drawn from scattered observations. In northern Peninsular Malaysia, Kromann-Clausen (2015) found a higher abundance of selected elephant-dispersed plant species (i.e., *Durio sp., Mangifera sp., Artocarpus integer, Monocarpia sp. Dillenia indica, and Sandoricum sp.)* nearer salt-lick hotspots, areas where elephant groups often visit (Hii, 2017). At the tallest mountain of Peninsular Malaysia, Gunung Tahan, a network of elephant trails can be found along the mountainside, leading up to a plateau where a rare sphagnum bog was found. Water-filled footprints and open water pools indicated high elephant activity, providing clues that the sphagnum bog was created by elephants, modified from what was originally an upper montane forest (Yao et al., 2009).

Olivier (1978) provided valuable information on food availability for elephants through the application of local indigenous knowledge from the Orang Asli in the Taman Negara rainforest. He found a higher percentage of foodplants available in the sampled secondary forest than in the primary forest. In the primary forest, trees made up 12% of the total food available, while palms made up 66% of the total food available. In secondary forests, trees made up 33% of the total food available, while palms made up 58% of the food available. Within trees, 37% were small trees in primary forests and 42.7% were small trees in secondary areas. Amongst palms, 73% were small palms in primary forests, while 34% were small palms in secondary forests.

Olivier (1978) referred to elephants of Southeast Asian rainforests as 'facultative palmivore'. He found elephants consumed a high amount of palms (44% of total mouthfuls consumed), followed by grasses (33%), trees (15%), and herbs (8%; stated as under-represented). Based on total elephant consumption and total vegetation available (Petrides, 1975), he calculated that elephants highly preferred grasses (calculated preference ratio 184), followed by herbs (7) and palms (4) while they avoided trees (0.2). Such discrepancies are unlikely and he recommended using an unbiased preference that could compare study areas meaningfully. In his study, elephant consumption was gathered from a combination of elephant feedings in the forest, and elephants supplied with food in the Jengka triangle and Krau Game Reserve (Kuala Lompat). Food availability was gathered from Taman Negara (primary forest) and Labis-Bekok (secondary forest: recovering from selective logging eight years before sampling). While these sampling methods were the best Olivier could arrange logistically for his study, it is unclear how these combinations could have indirectly affected the final calculations of preference ratios. For example, plants such as grasses are limited in the wild but were supplied for feeding trials.

In the Lower Kinabatangan Wildlife Sanctuary (LKWS), Eastern Sabah, English et al. (2014a) found high preference and utilization of grasses and gingers by the Bornean elephants *(Elephas maximus borneensis)* with the same preference ratio but restricted to only common elephant foodplants. In the Shangyong forest (Xishuangbanna, China) with a wet and dry season, Chen et al. (2006) counted stems from fresh elephant traces. They found browsing species were more frequently consumed when compared to grazing species (77 species taking 91% *vs.* six species taking 9%) in which early successional species constitute a more substantial proportion than late-successional species (42 species taking 59% *vs.* 32 species taking 37%). In Northern Peninsular Malaysia, Yamamoto-Ebina et al. (2016) inspected elephant dung using micro histological fecal analysis. In the primary forest, they found non-grass monocotyledonous leaves accounted for 22%, woody debris 32%, and woody fibre 20% of plant parts undigested in dung. In the logged forest, elephant dung is composed of 33% non-grass monocotyledonous leaves, 24% woody debris, and 26% fibre. Along the roadside, grasses (47%) were highly consumed.

The differences between Asian elephant diet studies call for a reassessment of their diet. Do trees make up only 15% of Asian elephants' diet in closed-canopy forests (Olivier, 1978)? Will Peninsular Malaysia elephants share similar habits as the Bornean elephants, consuming mostly grasses? **In *chapter two*, I revisited the diet of Asian elephants in both closed**

canopy and early successional forests recovering from shifting agriculture practice. I aim to distinguish the principal and preferred foodplants of Asian elephants in both habitats. To avoid biases, the calculation method of the preference ratios is modified to account for variability across all plots (see Chapter Two).

The lack of evidence for the influence of Asian elephants on forest structure sees the need to measure selective feeding as well as herbivory impacts by the elephants. Olivier promoted the consideration of differentiating stems into different age structures and sizes. Such information is essential to help determine the actual availability of foodplants in different forest types. More recently, Terborgh et al. (2015; 2016) have evaluated the impacts of megafaunal herbivory through the comparison of stem breaks in different size classes. **A difference in stem size feeding will help to determine whether Asian elephants exhibit selective feeding, and provide indications for the effects of Asian elephants in modifying the structure and composition of closed canopy**. **To understand the feeding behavior of Asian elephants, I examined the impact of Asian elephants on different plant types and sizes, how they damage stems (e.g., uprooting or stem breaking), and at what scale (impact per unit area) this occurs.** As mentioned earlier, tropical plant species have strong sprouting ability (e.g.,>50%) (Everham & Brokaw, 1996). Longer-term studies may reveal the growth rates of coppiced stems and how that could affect secondary productivity, structure, or composition of the forest. Thus, providing stronger evidence if Asian elephants act as filters of the tree recruitment process.

Other Ecological Functions of Elephants

Apart from regulating habitats, energy flow, physiochemical processes, plant nutrition, and the eventual secondary productivity of other consumers, elephants are also known to create physical trails and migration routes, dig wells to reach subsurface water, enlarge water basins, reshape caves to feed on mineral sediments, move a large amount of surficial materials, and trample and break down surface materials (Haynes, 2012). Their dung can sometimes house smaller animals such as amphibians (Campos-Arceiz, 2009) and beetles (Goh et al., 2014). Their geophagy (soil eating) behavior creates large natural licks in the rain forest (Klaus et al., 1998). From one year's camera trap observations (Hii, 2017), 165 visits by elephants were recorded, identifying 55 adults and 21 offspring in a well-utilised mineral lick. Salt licks are especially important for elephants, acting like nutrient pools and social hubs to female elephants and the young ones; regular visits result in lick enlargements and physical changes to the habitat. Indirectly, these visits could lead to forest composition changes over the longer term.

ELEPHANTS AS IMPORTANT SEED DISPERSERS

Amongst the existing studies on ecological function, the role of elephants as seed dispersers is relatively well established. Multiple studies across diverse landscapes support the elephants' importance in reliably, or effectively, dispersing large numbers and diverse types of seeds over long distances (e.g., Lieberman et al., 1987; Chapman et al., 1992; White *et al.* 1993; Yumoto *et al.,* 1995; Engel, 2000; Theuerkauf *et al.,* 2000; Nchanji & Plumptre, 2003; Campos-Arceiz & Blake, 2011). Seed dispersal is the active or passive process of a propagule moving away from the parent plant to where the propagule, usually a seed, comes to its final rest. Animal facilitated seed dispersal helps a plant spread its offspring both in magnitude and direction (Cousen et al., 2008). Ideally, effective dispersal ensures successful reproduction, measured as the number of new adults produced by the dispersal activities of a disperser. Empirically, effectiveness is projected as the number of seeds dispersed as a product of the probability that a dispersed seed can grow into a new reproductive adult, i.e., effectiveness = quantity x quality (Schupp, 1993) (*see chapter four*).

Seed Dispersal in African Forest Elephants

In the moist evergreen and semi-deciduous forests of Bia National Park of western Ghana, the African forest elephants helped disperse multiple fruit species from a diverse range of habitats, including closed and open forest, gaps, and swamp forests (Short, 1981). Amongst the fruits dispersed by the elephants, several were large-fruited species such as *Panda oleosa (family Pandaceae)*, *Balanites wilsonia (family Balanitaceae)*, *Strychnos aculeata (family Loganiaceae),* and *Parinari excelsa (family Chrysobalanaceae)* (Lieberman et al., 1987). In other national parks, some fruits depended highly on elephants for dispersal, such as *Hyphenae beguellensis*, *Ricinodendron rautanenii,* and *Schlerocarya birrea* from the Kalahari Sands habitats of southern Central Africa. In the Kibale National Park of western Uganda moist evergreen forest, *Balanites wilsoniana* suffered high mortality (84%) without elephants as dispersal vectors (Cochráne, 2003). In the Ndoki Forest, northern Congo, forest elephants appear to disperse more intact seeds than other large vertebrates. Blake et al. (2009) foresaw that the loss of elephants might lead to a wave of recruitment failure among animal-dispersed tree species, providing advantages for the regeneration of species-poor abiotically-dispersed guilds of trees.

Most of these studies, described above, recognise the importance of elephants to the recruitment and diversity of trees. On the other hand, Hawthorne & Parren (2000) concluded that the loss of African forest elephants had little influence on plant biodiversity in Ghana. Amongst 2000 species of forest plants, they found the role of elephants in promoting regeneration was low. At broader scales, the recruitment of these plants is also sustained by alternative dispersers. They suggested that elephants may be more important to disturbed landscapes where they are attracted to, aiding the dispersal and re-establishment of plants in these sites.

Elephants have an excellent memory and are efficient at searching for fruiting trees. In several systems, African forest elephants are known to create key foraging trails through the forest. Networks of trails connecting major fruit trees such as *Parinari excelsa, Balanites wilsoniana, and Tieghemella heckelii*, allow elephants to move quickly between fruiting areas (Short, 1981; Bia National Park, West Africa). At elephant trail intersections, fruit trees were highly abundant (Short, 1981; Blake & Inkamba-Nkulu, 2006). Vanleewé & Gautier-Hion (2002) classified these paths, which provide elephants with fruits and herbaceous foods, as 'foraging paths'. Other types of paths include the 'boulevards' that were used for long-distance (up to 34km) travel, linking favourite sites such as clearings and 'clearing alleys' that form a dense network of tracks around clearings.

Seed Dispersal in Asian Elephants

The Asian elephant is capable of dispersing seeds from 1.2km (Campos-Arceiz et al., 2008a) to 3.5 km, or more than 10km (Sekar et al., 2015). In Peninsular Malaysia, their home range is up to 600 km^2 (Wadey, 2019). In Myanmar, their movement behavior was linked to seasonal and geographic variation in the seed dispersal curves (Campos-Arceiz et al., 2008). According to Campos-Arceiz & Blake (2011), Asian elephants are seed dispersers for at least 122 fruit species from 92 genera and 39 families. Available seed dispersal studies of elephants, however, showed lower levels of frugivory and higher variation in the number of seeds dispersed by Asian elephants as compared to the African elephants. In Khao Yai national park of Thailand, for example, Kitamura et al. (2007) found Asian elephants dispersed the seeds of just a small number of plant species. Although seeds recovered from elephant dung were hard and came from fruit that ranged 23–63 mm in diameter, few were within measurements of the megafauna syndrome fruits, delineated by Guimarães et al. (2008) as fruits with diameter 4cm or larger. In the Nilgiri Biosphere Reserve, Southern India, Baskaran & Desai (2013) identified seeds of only eight plant species in 16% of 455 dung piles examined. Most fruit consumption occurred in the dry thorn forest, rather than in dry and moist deciduous forests. Elephants frequently consumed *Tamarindus indica,* and *Acacia intsia.*

Few elephant-dependent fruit species have been described in Asia. In the Buxa Tiger Reserve of India, Sekar (2014) found Asian elephants to consume more fruits of large-fruited species, such as *Dillenia indica, Careya arborea,* and *Artocarpus chaplasha,* than other animals. Being hard at its initial stage, *Dillenia indica* is primarily consumed and dispersed by elephants and perhaps other megaherbivores. Elephants were responsible for 63.3% of the fruits consumed by frugivores. Experiments on post-dispersal seed predation revealed that small insects (<3mm) significantly reduced the germination success of *Dillenia indica,* leading to the loss of 82% of *Dillenia indica* seeds from dung boluses (Sekar et al., 2016).

Campos-Arceiz & Blake (2011) suggested that the time difference that proboscideans inhabited Asia (23 mya) and Africa (60 mya) could have contributed to a higher adaptation as seed dispersers in African elephants. African elephants spread across a broad band of the equator where animal-mediated seed and seed sizes are large. Forest composition likely affected the availability of elephant-dispersed fruits as wind-dispersed dipterocarps dominate several Asian tropical forests. In some systems, quantity is not a key component of effective dispersal (Schupp, 1993). Could Asian elephants provide the seed dispersal service differently as compared to African elephants? Furthermore, what will their dispersal role be in the closed canopy rainforest?

Traits of Fruits Dispersed by Megafauna

From the neotropics, Janzen & Martin (1982) described megafaunal dispersal syndrome fruits as large, indehiscent fruits that contain sugar, oil, or nitrogen-rich pulp. The seeds or nuts of these fruits are often protected by a tough endocarp or seed coat that enables seeds to survive the effects of mastication or digestion by large mammals. Some seeds may be scarified and digested. Soft or weak seeds are often small or are nested within a hard core or nut (e.g. *Spondias*, *Scheela,* and *Hippomane* species). Some seeds are designed to block occlusion of the molar mill (e.g., *Guazuma ulmifolia*). In a given habitat, we may find fruits of different species at different times of the year. Fruits fall either unripe or shortly upon ripening, attracting terrestrial dispersers to feed. Such fruits attract few arboreal or winged animals unless there is a much larger fruit crop. When key megafauna dispersers are lost, these fruits often rot out under the parent tree crown. Lacking potential dispersers, seed predators such as peccaries, tapirs, agoutis, and small rodents sometimes act as dispersers. Free-ranging introduced horses, pigs, or cattle also feed on them. Natural habitats of megafaunal plants are often in forest edges adjacent to grasslands, alluvial bottoms, or gentle slopes accessible for megafauna. In Southwestern Costa Rica, these include plants such as *Astrocaryum standleyanum, Calophyllum macrophyllum, Hymenaea courbaril, Parkia pendula, Pouteria species, Raphia taegera, Scheelea rostrate, Simaba cedron, and Terminalia catappa.*

Guimarães et al. (2008) provided a size limit for megafaunal syndrome fruits. This includes fruits of diameter 4–10 cm with one to five large seeds and fruits of diameter greater than 10 cm having multiple small seeds (usually >100 seeds), characterised with distinct fruit diameter, mass, and seediness. Fruits within this range are represented from unrelated families such as Sapotaceae, Fabaceae, Solanaceae Apocynaceae Malvaceae, Caryocaraceae, and Arecaceae. With megafauna extinction from South America since 10,000–15,000 years BP, these fruits continue to persist, but potentially with increasing aggregation, reduced geographic ranges, limited genetic variation, and increased among-population structuring (Guimarães et al., 2008).

As one of the last surviving megafauna, elephants are likely important dispersers for several megafaunal syndrome fruits in the Sundaic region. No comprehensive study has been made of megafaunal fruits in this region. Fruits dependent on Asian elephants for dispersal are notably lacking in equatorial rainforest less than 10 degrees in latitude (Campos-Arceiz & Blake, 2011). In Malaysia, no detailed frugivory and seed dispersal study was carried out on fruiting wild elephant-dispersed trees. **In *chapter three*, I evaluated the interactions of Asian elephants and other animals of a large-fruited species, the *Irvingia malayana*. This study helps fill knowledge gaps of both quantitative (number of visits) and qualitative (seed treatment and success of germination) aspects of Asian elephant seed dispersal in a Sundaic rain forest.**

SEED DISPERSAL COMMUNITY AND MUTUALISTIC NETWORKS

While we recognise the significance of understanding the functions of the elephant through an ecosystem approach, it appears up until now that quantifying seed dispersal alone remains difficult in practice. At the rate that we are losing elephants and suitable habitats, understanding their effects in a broader context is highly unachievable. **In *chapter four*, I thus opted for an interdisciplinary approach to determine the seed dispersal role of Asian elephants and other animals at a community level.** I achieved this by gathering data of frugivory and seed dispersal interactions through a combination of field observations, measured fruit traits, local ecological knowledge (LEK), and published records. **The introduction of the local indigenous people and the importance of LEK were highlighted in chapters four and five.** Mutualisms, including seed dispersal interactions, are increasingly understood through a network perspective (Bascompte Jordano, 2014). **I tested the hypothesis that Asian elephants hold high functionality within the seed dispersal community in a highly diverse network.**

Network Structures and Functionalities

Network studies help us visualise and understand the mechanisms driving mutualistic interactions. Networks applicable to our daily lives include social, transportation, communication, computer, and epidemiological networks. Ecological networks include species-level interacting networks such as food webs (e.g., Camerano, 1880; Power, 1992; Dunne at al., 2002a, 2002b; Montoya & Solé, 2003), pollination (Memmot et al., 2004; Olesen et al., 2007; Ramos-Jiliberto et al., 2010), and seed-dispersal networks (Vidal et al., 2013; Dugger et al., 2017; Timóteo et al., 2018). Ecological networks allow for the identification of important species to the network (e.g. Palacio et al., 2016; Escribano-Avila et al., 2018). A famous textbook example concerns the collapse of the cod population in the north-western Atlantic in the eighties. To control predation, seals were largely hunted during the nineties, yet the cod population could not recover. Studying the food web that connects cod and seals, ecologists found seals to be a key predator to several other species that predate cod. Killing seals, thus, can end up increasing the pressure of cod predation from other species (Bundy et al., 2009).

Graph theory is used to generate the structure and properties of networks (Leonard Euler 1736; Erdös & Rényi, 1959). Graphs are unipartite (one-mode), bipartite, or tripartite. Within ecological networks, unipartite graphs such as trophic networks may consist of animals interacting with one another. Bipartite graphs are mutualistic graphs such as seed dispersal networks, where nodes link a plant and an animal that are not within the same trophic level (or group). Tripartite networks exist in super-parasitoids interactions (Bascompte & Jordano, 2014).

Complexity is a key feature of networks. **In chapter four, an analysis of the seed dispersal interactions at the network level will allow us to describe the structure and resilience of the seed dispersal network, and how the network properties are associated with key interactors.** Different measures have been used to describe the properties and structure of these networks – each providing information concerning elements supporting the organisation of the system. Modularity, nestedness, and connectance are focal metrics studied in several ecological networks. Modularity defines the 'community structure' of a network. Studies on modularity facilitate our understanding of system structure, stability, and persistence (Stouffer & Bascompte, 2011; Bascompte & Stouffer, 2014). Nestedness infers a stronger organisation. In a nested network, a few species control a high number of interactions. The most generalised species (with high degrees) tend to interact among themselves, creating a core in the matrix, while the specialized species (with low degree) interacts with species subset in the core. The core of generalists may share roles akin to one another in ecosystem functionality. This presence of functional redundancy ensures system persistence while some species go extinct (Bascompte & Jordano, 2014). Connectance (C) describes the proportion of realised interactions in the network. In mutualistic networks, higher connectance and nestedness is expected when interaction overlap is high. Such networks are also more robust to extinctions (Mello et al., 2011). Regardless of the type of networks, nestedness and modularity decrease with increased connectance (Fortuna et al., 2010).

In a community, not all species maintain key roles in species interactions. **On top of assessing the role and importance of Asian elephants, I was also concerned about identifying other seed dispersers important to the network.** In networks, 'hubs' and 'connectors' are commonly related to high functionality. 'Hubs' are highly linked nodes that emerge out of scale-free properties, when heterogeneity arises from a set of regular behavior and order in real-world networks (Albert & Barabási, 2002). 'Provincial hubs' connect nodes in the same module, while 'connector hubs' connect several modules within the network (Guimerà & Amaral, 2005). When structurally important hub or connector species go extinct, modules may break apart, leading to extinction cascades (Olesen et al., 2007).

Seed Dispersal Networks

Seed dispersal networks are represented by interactions linking plants and their dispersers. Amongst available seed-dispersal network studies, most are avian focussed, in which hornbills represent the larger-bodied representative (Mello et al., 2011; Schleuning et al., 2011; Dugger et al., 2017; Costa et al., 2018). Some include animals such as primates, bats, and wild boars (Mello et al., 2011). Existing seed-dispersal network studies are mainly from Neotropical or Afrotropical systems (Schleuning et al., 2011; Dugger et al., 2017); few are from the Oriental region (Schleuning et al., 2011; Escribano-Avila et al., 2018). Networks including large vertebrates are rare (Vidal et al., 2013), and even fewer are community-oriented (e.g., Donatti et al. 2011; Timóteo et al., 2018). Tropical studies that have explored community-based networks include the study of the spatial structure of seed dispersal across different habitats in Mozambique (Timóteo et al., 2018), invasive species in the Galápagos (Heleno et al., 2013), the restoration of the seed dispersal function in the Gorongosa National Park, Mozambique (Correia et al., 2017), the seed dispersal network of the Aldabra atoll (Wilfredo et al., unpubl.) and the network of the hyper-diverse community of Brazilian Pantana (Donatti et al., 2011).

The Neotropical Brazilian Pantanal seed dispersal networks described seed dispersal interactions from three different habitats spanning gallery forests, savannahs, and semi-deciduous forests (Donatti et al., 2011). It was amongst the first community-oriented networks that included several mammals, reptiles, fishes, birds, and the plants they disperse. The networks were found to be nested and modular, comprising of five distinct modules. Within the community, large-vertebrate seed dispersers such as the feral pig (*Sus scrofa*) and tapir (*Tapirus* *terrestris*) served as highly-linked hubs, while the howler monkey (*Alouatta caraya*), a plant *Genipa americana* (Rubiaceae), and *Chaco chachalaca* (Ortalis canicollis, Cracidae) acted as connectors linking these modules. Amongst the modules, only one mammal-dominated module showed nestedness. They attributed the non-detection of a nested pattern as an artefact of low species numbers. Missing in the community is the presence of a megaherbivore.

Network studies could only provide a snapshot of the overall seed dispersal hierarchy and roles of the system. Many network metrics are secondary covariates rather than causative factor of the underlying mechanism (James et al., 2012). Simpler metrics should accompany network analysis (e.g., number of mutualistic partners a species has) to determine the mechanisms driving higher-order network properties (James et al., 2012). Seed dispersal network patterns are driven by key interactions between animals and the plants they dispersed and how animals handle seeds so that they are effectively dispersed (Schupp, 1993). Complex fruit processing by different dispersers creates manifold seed fates. **In chapter four, I recognised the importance of different seed dispersal methods between different seed dispersers and identified key complementary seed dispersers in the system.** Most inferences were based on existing seed dispersal studies.

Seed Dispersal Interactions in Asia and Sundaland

Many seed dispersal interaction studies are available in Asia. There is also a recent increase in individual species-oriented studies to a broader frugivore community (McConkey, 2018). For example, studies between plants and primates, hornbills, squirrels, and pigs in Indonesia (Marshall et al., 2014), birds, squirrels, civets, gibbons, macaques, bears, deer, and elephants in Thailand (Kitamura et al., 2002; Brodie et al., 2009; McConkey & Brockelman, 2011; Chanthorn et al., 2017) and birds, primates, squirrels, and ruminants in India (Ganesh & Davidar, 2005; Datta & Rawat, 2008; Prasad & Sukumar, 2010). Amongst these studies, Kitamura et al. (2002) described interactions with the broadest community of animals; encompassing 259 fruits from 65 families, dispersed by bulbuls, the *Ducuala badia* pigeon, hornbills, squirrels, civets, gibbons, a macaque (*Macaca nemestrina*), bears, deer, and the Asian elephant in the Khao Yai National Park, north-eastern Thailand. From comparisons of dietary overlaps and characteristics of fruits, they found most fruit species were consumed by a variety of frugivores, with small-seeded and soft fruits being consumed by a broader group of frugivores. Large single-seeded fruits are consumed by few dispersers and are avoided by small frugivores that thrive in degraded forests. **More elaborate seed dispersal interactions associated with specific seed disperser species and taxa are described in chapter four.**

The role of large vertebrates in seed dispersal is well recognised (E.g., Terborgh, 2008, Mueller et al., 2014; Nakamura & Itoh, 2015; Naniwadekar et al., 2019), but is incomplete in network studies (Vidal et al., 2013). To my knowledge, ***chapter four*** **is the first community-oriented seed dispersal network study in the Sundaic region. I discussed the organisational patterns and functional differences that emerged when the Asian elephant, other megafauna, and large mammals are present in the network.** Living amidst a global wave of biodiversity loss where large animals are highly threatened (Hooper et al., 2005; Dirzo et al., 2014), this is an important chapter providing insights into the robustness and functionalities of megadiverse seed dispersal communities, particularly to the Sundaic region. **I examined the consequences of defaunation to coextinctions of the loss of ecological service provided by the interacting species. As this topic requires further exploration, the results were further discussed in chapter five – the general discussion chapter.**

THESIS AIM AND OBJECTIVES

In this thesis, I aim to understand the ecological function of Asian elephants in the Sundaic region through their herbivory and seed dispersal interactions with the environment in four key themes: (1) diet selection, (2) herbivory impacts, (3) frugivory, and (4) their seed dispersal role in the community. The process involved working with collaborators and the team to gather the data required to answer the research questions. **In chapter one,** I covered a review of the ecological functions of African and Asian elephants and identified the knowledge gaps I aimed to fill with regards to Asian elephants in the Sundaic rainforests. **In chapter two**, I determined if elephants exhibit selective browsing that could potentially affect the forest structure in longer terms. This is accomplished by documenting the different types and sizes of plants consumed and damaged by Asian elephants in two different habitat types — closed forest and early successional forests, measuring the Asian elephants' (1) principal diet, (2) food preference, and (3) herbivory impacts. In **chapter three**, I quantified the importance of Asian elephants to the dispersal of a large-fruited species, *Irvingia malayana*, by differentiating the interactions of the vertebrate consumers and determining the germinability of seeds dispersed by Asian elephants. **Chapter four** allowed for a broad understanding of the seed dispersal community of the Sundaic rainforest ecosystem, and the influence of Asian elephants. I (1) described the structure of the seed dispersal network, (2) identified functionally important seed dispersers, (3) evaluated the role of Asian elephants, and examined (4) the effects of defaunation on functional coextinctions to the network. The key findings of this thesis were summarised in **Chapter five**. I discussed studies that can be explored and refined to improve our understanding of the function of Asian elephants in the Sundaic ecosystems. Very importantly, I discussed the importance of local ecological knowledge (LEK) and how the knowledge and heritage of the Orang Asli, requires immediate action to prevent further erosion.

CHAPTER TWO

Diet Selection and Herbivory Impacts of Asian Elephants in Peninsular Malaysia

ABSTRACT

Little is known about the ecological influence of Asian elephants (*Elephas maximus*) in tropical rain forests. In a previous study, we found a lower density of tree saplings and palms in a forest with elephants (Belum) than in a forest where elephants were absent since 1993 (Krau). To ascertain if selective browsing by Asian elephants contributes to the differences in forest structure, this study documented elephants' diet selection and herbivory impact in two habitat types common to Malaysia's rainforest – closed forest (F) and early-successional shifting agricultural habitats (ES). Elephant foraging was highly selective, favouring monocots, especially, palms (preference ratio, PR=4.6, N=20 patches). Despite monocots (16%, n=10 patches) were rare in closed forest, elephants consumed a large amount of palms (39±29%) (n=24 observations, obs.). Where monocots are available, herbs (87%, n=6 patches) and palms (72%, n=3 patches) sustained high damages. Hindgut fermentation allowed elephants to consume large amounts of trees (30±24%) as part of their principal diet. In foraged plots, a high number of tree saplings were broken (14 stems 100 m^{-2}, n=20). In early-successional patches (n=6 patches), monocots above 1m were not abundant (14%), and the availability of palms was low (4%). Elephants fed on a high amount of trees (40±22%, n=16 obs.) largely represented by Euphorbiaceae (e.g., *Macaranga* and *Mallotus* spp.), and large tree saplings sustained high damages (41%, n=11 patches; 12 stems 100 m^{-2}, n=13). Across both habitat types, tree saplings broken by elephants were around 2 ±1 cm in stem-width (up to 7 cm, n=190 stems). Many palm species are slow-growing and adapt to different soil conditions. In the Belum rainforest, relentless selective herbivory on palms can lead to a reduced palm density, keeping them rare. Most tree saplings, however, can resprout following damages. Elephant's role in structuring mature closed forests thus may be insignificant. Apart from elephants, wild boars harvest a large number of woody plants for nest building. We require considerations of stem breaking by both species to account for the effects on forest structure. Stem breaking may appear destructive, but this process can facilitate the productivity of the forest, and increase food availability to other herbivores. The effects of elephants in early-successional habitats that are tied with factors such as the growth rates of plants, the recursive feeding patterns of the elephants, and their relationship to shifting-agricultural gap sizes and locations can be further explored.

BACKGROUND

Elephants are ecosystem engineers, organisms capable of modifying or maintaining habitats with strong ecological influences on other species (sensu Jones et al., 1994 Wright & Jones 2006; Haynes, 2012). Their herbivory impacts have been shown to exert top-down pressure on vegetation, forest structure, and diversity; reducing the density of saplings, impeding tree recruitment, and maintaining woodlands or grassland ecosystems in stable states (Dublin et al., 1990; Holdo, 2006; Lawes & Chapman 2006; Terborgh et al., 2016).

The influence of elephants on plant communities and forest structure is linked tightly to their foraging habits and dietary needs. As megaherbivores, elephants can consume about 150kg or 10% of their body mass to meet their daily needs, foraging 12 to 19 hours a day (Vancuylenberg, 1977; Sukumar, 2006). Asian elephants are distributed discontinuously across Asia, with habitat ranges from 50 to 150 km^2 in Sri Lanka, and 34 to 3708 km^2 in India. In Peninsular Malaysia, their home range is up to 600 km^2 (Wadey, 2019). These ranges span areas with highly varied vegetation and climate (Sukumar, 2006). Being a mixed feeder consuming both grass and browse (Sukumar, 2003), their diet and foraging strategy differ with landscape differences and seasonality (e.g., Sukumar, 1990; Chen et al., 2006; Prajapati, 2008).

Early-successional or pioneer plant species such as grasses, legumes, sedges, spurges, figs, and buckthorns are common elephant food (McKay, 1973, Chen et al., 2006, English et al., 2014). In grass-dominated habitats, the diet of Asian elephants may constitute mainly grasses. The palatability of grasses at various stages of growth throughout the year affects the way elephants feed; whether selecting for leaf blades after first rains, uprooting tall fresh clumps as treats, or discarding tougher leaves for the succulent basal stems when they mature (Sukumar 1990). In mixed-grass and browse habitats, their diet includes both grass and woody species. At times, more woody species are consumed, at times, more grasses are consumed. The proportions eaten may also alternate with seasons (Sukumar, 1990; Steinheim et al., 2005; Joshi & Singh, 2008; Koirala et al., 2016).

In tropical rainforests where grasses are less abundant, browsing species and fruits may make up most of an Asian elephant's diet (Chen et al., 2006, Campos-Arceiz & Blake, 2011; Yamamoto-Ebina et al., 2016). Olivier (1978) recorded up to 400 plant species eaten by elephants in Malaya and Sumatra, identifying palms as the most important foodplant of Malayan elephants. In a recent study, however, English et al. (2014) found high preference and utilization of grasses and gingers by the Bornean elephants *(Elephas maximus borneensis)* in the Lower

Kinabatangan Wildlife Sanctuary (LKWS), Eastern Sabah, Malaysia. The study of Asian elephants' diet or herbivory impacts in the rainforest remains challenging with difficulties in locating wild elephants and making direct observations. Retrieving information of diets with indirect methods such as faecal analysis (Chen et al., 2006; Yamamoto-Ebina et al., 2016), local ecological knowledge (Olivier, 1978; Campos-Arceiz et. al., 2008), and impacts from stem breaks (Chen et al., 2006; English et al., 2014; Terborgh et al., 2018) are useful methods but may present biases as a result of limited clues available (e.g. quantifying the exact number of stems eaten or uprooted). Direct observations with captive wild elephants present as a good alternative to attaining this information (sensu Olivier, 1978).

Studies on the African forest elephants may provide useful references to the foraging habits and impacts of forest-dwelling Asian elephants. In closed canopy Afrotropical forests, browse appeared less important than fruits (Short, 1981; White et al., 1993; Blake et al., 2009), and the local and regional fluctuation of elephant densities was linked to fruit availability (White 1994). Networks of trails connecting fruit trees provide the forest elephants with quick access to abundant fruits and also herbaceous foods (Short, 1981; Vanleeuwé & Gautier-Hion, 2002; Blake & Inkamba-Nkulu 2006). To browse in closed forests, elephants need to leave trails and push through bushes to feed. The forest elephants preferred browsing in open forests and maintained gaps (Short, 1981; Struhsaker et al., 1996; Vanleeuwé & Gautier-Hion, 2002). Breaking of main stems, de-barking, uprooting, and pushing over of trees were less common as compared to the African bush elephants (*Loxodonta africana*) where feeding has led to major landscape changes (Beuchner et al., 1963; Short, 1981; Western, 1989). Much of this knowledge, including browsing impact, is unavailable in rainforests where Asian elephants live.

Available studies from dry forests have shown that woody-plants of different stem sizes were damaged by Asian elephants including both small stems below 10 cm in diameter (Ishwaran, 1983), as well as larger stems up to 16 cm (Pradhan et al., 2007). Some impacted trees such as *Mallotus phillippinensis* continued to persist after being pushed over. Branch breaking, main-stem breaking, and stem twisting were observed on damaged woody plants (Ishwaran, 1983).

The Malaysian rainforests are characterized by dry-fruited trees from the *Dipterocarpaceae* family which dominate the canopy cover, as well as forest basal area (Davies et al., 2003; Caldecott & Caldecott, 1985; Frechette, 2014). Other common families include both dry and fleshy-fruited species such is found in the Fabaceae, Euphorbiaceae, Burseraceae, and Anacardiaceae families (Sakai et al., 1999). The phenology and productivity of fruits tied with food availability for terrestrial animals, are yet to be investigated. The diversity and volume of seeds dispersed by Asian elephants in tropical rainforest appear to be considerably lower (e.g. Kitamura et al., 2002; Kitamura et al., 2007 in Thailand; Campos-Arceiz et al., 2008 in Myanmar; Varma et al., 2008 in Vietnam) than seeds dispersed by Asian elephants in the seasonal forest (e.g., Sri Lanka; Samansiri & Weerakoon, 2007) and African elephants in African landscapes (Gautier-Hion et al., 1985; Blake et al., 2009; Babweteeraa et al., 2007). The importance of fruits in the forest-dwelling Asian elephant diet may thus be less significant than browse. How Asian elephants may respond to mast fruiting and the identification of more fleshy-fruited tree species that mast-fruit remains to be further investigated (Appanah, 1985; Sakai et al., 1999; Sakai, 2002).

Grass is virtually absent from the Sundaic forest, except in gaps maintained by shifting-agriculture practices. Bamboos, palms, and large herbs edible to elephants are either scattered amongst understory plants, found in micro-habitats such as ridge tops or rivers or exist in heterogeneous populations in the forest. At present, logging and development have led to extensive forest degradation and the clearings of good wildlife habitats (e.g. riparians habitats). The alterations of lowland habitats crucial for large terrestrial animals to human-dominated landscapes follow with the silencing of animals' functionality in our systems - much of which is lost before comprehensive studies can be assessed. Our lack of understanding could impede the proper management of elephants in landscapes facing the rise of human-elephant conflicts, where mitigations are required. With less than 2000 wild elephants estimated to be left in Peninsular Malaysia (Saaban et al., 2011), we require a clear picture of the Asian elephants' diet and preferences, an estimation of elephant foodplant availability, and indications of their influence in structuring the rainforest.

In a previous study on the foraging impacts of Asian elephants, we found lower densities of palm and tree saplings in elephant-present forest patches, indicating a possible influence of Asian elephants on forest structure (Terborgh et al., 2016). To ascertain if these differences are likely due to the effects of selective browsing, here, my collaborators and I followed up with a study to understand the feeding ecology and impacts of forest-dwelling Asian elephants. We made direct observations on elephant feeding to document the (1) food consumed by Asian elephants, (2) their food preferences, as well as their (3) herbivory impact in two different habitat types: closed forest and early successional forests. I expected elephants to consume a large number of palms and dicotyledonous (dicots) tree saplings and impose high impacts on these stems in closed forests (inferring John et al., 2016). In early successional forests, I expected elephants to consume a large number of monocotyledonous plants (monocots), while the impacts on trees will be lower than in closed forests (inferring Sukumar 1990; English et al., 2014).

METHODS

Study Area

Krau Wildlife Reserve (KWR; 3º43'N, 102º10'E) is located east of the Titiwangsa Range in the State of Pahang, in Peninsular Malaysia (Fig. A2.1). It covers approximately 620 km^2 of protected forest, ranging from lowland to hill dipterocarp, and montane forest (Nizam, 2006). The landscape of KWR has an additional layer of complexity due to the presence of small-scale shifting agriculture by indigenous communities, a practice that introduces heterogeneity within KWR. These forest patches were cleared for crops alongside fruit gardens where trees were selectively replaced with favored fruit trees such as durian (*Durio* spp.), *kepayang* (*Pangium edule*), and rambutan (*Nephelium lappaceum),* enhancing vertebrate diversity and density within these patches (Moore et al., 2016).

We conducted our work at the southern border of KWR, besides the Kuala Gandah National Elephant Conservation Center (NECC). The forests in this area are mostly secondary lowland dipterocarp forests, with a mixture of older growths. We conducted our observations in patches of two different habitat types: (1) ten closed forest, and (2) seven early-succession habitats. The closed forest was largely undisturbed lowland dipterocarp forest (Fig. 2.01). The early-succession habitats consist of a matrix of forest edge and shifting agriculture sites belonging to different recovery stages (Fig. 2.02). These sites harbour gap characteristics; some with an understory dominated by grasses and pioneer plants saplings, others with shrubs growing amidst coppiced tree stands from shifting agriculture clearing practice.

The Kuala Gandah NECC, under the Department of Wildlife and National Parks (DWNP), is managed by the Elephant Capture and Translocation Unit for the protection and conservation of translocated wild elephants. Apart from protecting and translocating wild elephants from human-elephant conflict areas, NECC also cares for some resident elephants (Rahman et al., 2010). These elephants are kept in captivity and are only sporadically taken to the nearby forest.

Figure 2.01 Elephants feeding in closed forests.

Figure 2.02 Elephants feeding in early-successional habitats of shifting agriculture practice.

Data collection

Feeding observations – We conducted direct feeding observations on five wild-born captive female elephants of different ages from the Kuala Gandah NECC (Table A2.1). On each trip, two or three elephants were observed by the team. Elephants were directed by the mahouts to the chosen sites where they were left to feed freely (Fig. A2.2). Under the mahouts' supervision, we were able to stand approximately five meters away from the elephants to observe their feeding.

We conducted forty 30-minutes observations, recording an elephant's diet as the number of trunkfuls of plants consumed. Monocots were assigned as four main plant types: bamboo, herb, grass, and palm; splitting them into small monocots (< 1 m tall) or large monocots (≥ 1 m tall). Dicots including trees and lianas were classified as seedlings (< 1 m tall), small saplings (≥ 1m tall, < 1 cm in diameter), large saplings (dbh, diameter at breast height ≥ 1 cm and <10 cm), and dicot trees (dbh ≥ 10 cm). To differentiate foodplants from other broken stems, stems were tagged used (eaten), and unused (uneaten) with different paper tags (Fig. 2.03).

Figure 2.03 Stems accidentally broken (red tag, left) by resting elephant beside his mahout, Eddy. Eaten plant tagged yellow (right).

Patch description – To describe forest structure, herbivory damage, food availability, and elephants' food preference, we measured stems in three 2-m-radius circular patches at each site (Fig. 2.04). This patch size was chosen as elephants had fed on few dicot trees, and it enabled us to capture a considerable amount of information to describe the elephants' foraging impact with limited time to differentiate fresh evidence of elephants' impact. At each site, three patches were measured, including one undisturbed control patch (i.e., areas unaffected by elephant foraging) and two foraged patches. In the closed forest (F), we measured 20 foraged and 10 undisturbed forest patches. In early successional habitats, we measured 13 foraged and 6 undisturbed patches. Two ES sites were close to each other; so between them, we only sampled four patches (one undisturbed and three browsed). Within the patches, we measured only plants ≥ 1m tall. It was difficult to quantify plants below 1m, many of which could have been uprooted by elephants, leaving little trace of damage as compared to saplings. We differentiated plant types and measured stem diameter for all plants counted. We also recorded the height and diameter at which elephants damaged stems, if the plants are "used" (tagged eaten), and the type of herbivory damage incurred.

Figure 2.04 Circular patches (left) and field assistant, field assistant Ridzuan measuring a stem.

Herbivory damage – Herbivory behaviour includes six categories: i.e., leaf stripping, branch breaking, stem breaking, debarking, uprooting, or pushing overs of trees (Fig. A2.3a to 2.3i). Most grasses were assigned "stem breakage" rather than "uprooted" due to their extensive underground root system and dense aboveground growth. It is worth noting that in grassland habitats, elephants can feed on just the leaf blades, uproot plants for fresh leaves, or the entire clump for the succulent stems while discarding fibrous blades (Sukumar, 1990). Within the foraged plots, only stems that were debarked, broken at the main stem, pushed-over, or uprooted by elephants were measured as impact. Branch breakage and leave stripping were excluded. The mean size and heights of stems broken by elephants were measured from tagged plants, including plants that were outside sampled circular patches.

Statistical Analyses

Principal food vs Preferred food – I followed Petrides (1975) concept that principal foods are foods consumed in the greatest quantities. Preferred foods are foods more frequently consumed than are available in the environment. In this study, I determined the principal food of an elephant by counting the trunkfuls consumed per 30 minutes of observation. Preferred food is derived from what is consumed in proportion to the plants' availability in the environment (by patch measurements). The key calculations were calculated as:

Principal Food – Highest mean number of trunkfuls consumed per 30 minutes of observation.

Availability of Plants – The availability of plants across the landscape is represented by the relative availability (RA) of plants scaled to 100 m^2 in unforaged patches (**RA***unforaged*) in which:

$$\textbf{RA}\textit{unforaged}\textbf{, relative availability} = \frac{Na,\ number\ of\ available\ plants\ of\ a\ given\ type}{Ta,\ total\ number\ of\ available\ plants\ across\ all\ types}$$

$$\textbf{Percentage availability} = \textbf{RA}\textit{unforaged} \times 100\%$$

Food *Preference* – I calculated plants' preference using relative use (RU) of plants as a fraction of their relative availability (RA) in foraged patches, modifying methods from English et al. (2014) and Olivier (1978) in which:

$$\textbf{PR, Preference ratio} = \frac{RU}{RA}$$

$$\textbf{RU, relative use} = \frac{Nu,\ number\ of\ times\ a\ plant\ type\ was\ eaten}{Tu,\ total\ number\ of\ plants\ type\ eaten\ across\ all\ plant\ types}$$

$$\textbf{RA}\textit{foraged}\textbf{, relative availability} = \frac{Na,\ number\ of\ available\ plants\ of\ a\ given\ type}{Ta,\ total\ number\ of\ available\ plants\ across\ all\ types}$$

Data setup – In each observation, a "0" was assigned to a nominal variable to account for "no consumption." For example, when no grass was eaten in a feeding observation, I assigned "0 trunkfuls" to the category. I also assigned a "0" to a nominal variable when a plant type was absent from the patches. For example, if bamboo was absent, I assigned "0 stem" to the category. This helps describe the true diet of elephants and the availability of plants in the forest. As an exception, no "0" was assigned when plants are unavailable for preference analysis (i.e., calculating preference index using relative use and relative availability in foraged patches). Assigning "0" to preference when plants are unavailable could distort interpretations; such that a plant will be misinterpreted as avoided instead.

Descriptive Analyses – For measurement variability, I summarized the results with means ± standard deviation (SD) of either observation (obs.), patches, or measurements of the heights or diameter of plants. For diet, a total of 40 feeding observations were made – 24 in closed forest, 16 in early successional sites. For preferred food, forest structure, and forest structure impact, a total of 33 patches were measured – 20 in closed forest, 13 in early successional sites. The number of patches (n) for each plant type varied according to detection (as explained in the previous paragraph). For the availability of plants, 16 patches were measured – 10 in closed forest, 6 in early successional sites. For measurements of break diameter and height, 190 stems were assessed. To avoid confusion, I specify the units (i.e. observations, patches, stems, cm, m) for total samples (N) or sub-samples (n) at the start of each paragraph when presenting results. ***Models*** – To test for the effects of plants, plant sizes, and habitat differences on elephant diet, I set the discrete response variable of the models as "number of trunkfuls consumed" per observation. The fixed factors include "plant class", "plant type", "plant size", and "habitat". The variable "plant class" is a two-level nominal variable consisting of monocots and dicots. "Plant type" is a six-level nominal variable consisting of bamboo, herb, grass, liana, palm, and tree. "Plant size" is a six-level nominal variable consisting of small monocots (<1m tall), large monocots (≥1m), dicot seedlings (<1m), dicot small saplings, dicot large saplings, and dicot trees. The variable "habitat" is a two-level nominal variable of closed forest (F) and early-successional (ES) habitats. All plant variables are nested within the variable "habitat".

I relied on Microsoft excel, version 2004, and the R statistical environment 3.5.3 (R Core Team, 2019) for data analysis. Data were summarised with the *plyr* package (Wickham, 2011), and graphs were created using the *ggplot 2* package (Wickham, 2016). I checked data distributions with the fitdistr function (package *MASS*; Venables & Ripley, 2002). For normally distributed data, I examined elephants' diet with linear mixed-effects models using the *lmer* function (package *lme4*; Bates et al., *2015*). Since I conducted multiple feeding observations for each elephant, I included "elephant" as a random effect in the models. To include random effects, handle overdispersion, and high variation in count data, I used generalized linear mixed-effects models for data that fitted the negative binomial distribution using the *glmer.nb* function (package *MASS*). In circumstances where convergence was not possible – an implication of inadequate sample size to account for the factors included, I use the 'optimx' optimizer instead of the default 'Nelder-Mead' (package *optimx*; Nash & Varadhan, 2011). If further errors occurred, I examined the models using negative binomial generalized linear models, leaving out the random effects. Pairwise comparisons were carried out using post-hoc Tukey HSD tests with the *emmeans* function (package *emmeans*; Lenth, 2018). I examined plants' availability (% availability and stems 100 m^{-2}) using penalized quasilikelihood (PQL) for log normal data using the *glmmPQL* function (package *MASS*).

Simulated Preference and Impacts **–** I was unable to fit preference (PR) and impact on stems into any distribution, likely due to the absence of information (plant class or type undetected) in the small patches measured. I thus simulated preference ratios and stem impacts from the field data to compensate for the small sample size captured in certain plant categories and to provide a conservative estimation for the results. With Bayesian probability density functions using

Markov chain Monte Carlo (MCMC) methods, a credible interval and range were estimated for each plant type in its respective habitat (package *wiqid*; Meredith, 2018). PR-*simulated* are simulations of preference ratios, and impact-*simulated* are simulations of impact. 2016).

In previous studies, Olivier (1978) and English et al. (2014) obtained preference ratios based on plants gathered across the whole study. In this study, I modified the preference ratios to account for variability (PR-simulated ± SD) across all patches. In the appendix (Table A2.2), I presented calculations (PR*reference*) for the methods used by English et al. (2014) and Olivier (1978). In their studies, the preference ratios were limited to elephant foodplants (Olivier 1978), and commonly eaten species (English, 2014). In this study, we studied the preference ratio for all plant categories, without any prior selection of plants known to be consumed by elephants. As a result, precaution needs to be taken in comparing preferences between these studies.

RESULTS

This study facilitates an understanding of the influence that herbivory by Asian elephants can have in dipterocarp rainforests. I recorded the diet selection and herbivory impacts of five captive wild Asian elephants in two habitat types characteristic of Malaysia's forests i.e. closed canopy forest and early-successional shifting agricultural habitat. I identified selective browsing by (1) high consumption of a plant type or (2) preferred consumption of a less-abundant plant. Different sizes of monocots (bamboos, herbs, grasses, palms) and dicots (lianas, trees), and herbivory behaviour were recorded. Amongst the different herbivory behaviour recorded, only stems that were broken at the main stem or uprooted were considered as impacted stems in foraged patches.

Diet Composition – During direct observations (N=40 obs.), elephants consumed similar amount of monocots (48±27%) and dicots (52±27%) (df=1, X^2=0.0334, p=0.855) (Appendix model 2.1). The differences between monocots and dicots consumed were not pronounced between different habitat types (df=1, X^2=1.59, p=0.207)(Table 2.2 and 2.3)(Appendix model 2.2). Elephants consumed a greater amount of trees (34±24%) and palms (34±30%) than lianas (18±18%), grasses (6±16%), herbs (5±11%) and bamboos (4±14%) (df=5, x^2=68.9, p=1.763e^{-13}) (Table 2.1)(Appendix model A2.3). In closed forest sites (n=24 obs.), they consumed a higher amount of palms (39±29%) and trees (30±24%), than lianas (20±22%), bamboos (7±18%) and herbs (4±13%). No grass (0±0) was eaten (Fig. 2.05, Table 2.2). In early succession sites (n=16 obs.), they ate larger amounts of trees (40±22%) and palms (25±30%), as compared to grasses (15±23%), lianas (15±10%), herbs (5±9%) and bamboos (0±0%) (Fig. 2.05, Table 2.3). Grass consumption was proportionally higher in early-successional habitats than in closed forests; while bamboo was higher in the closed forest (df=5, X^2=42.4, p=4.86e^{-8})(Table 2.2 and 2.3)(Appendix model 2.4).

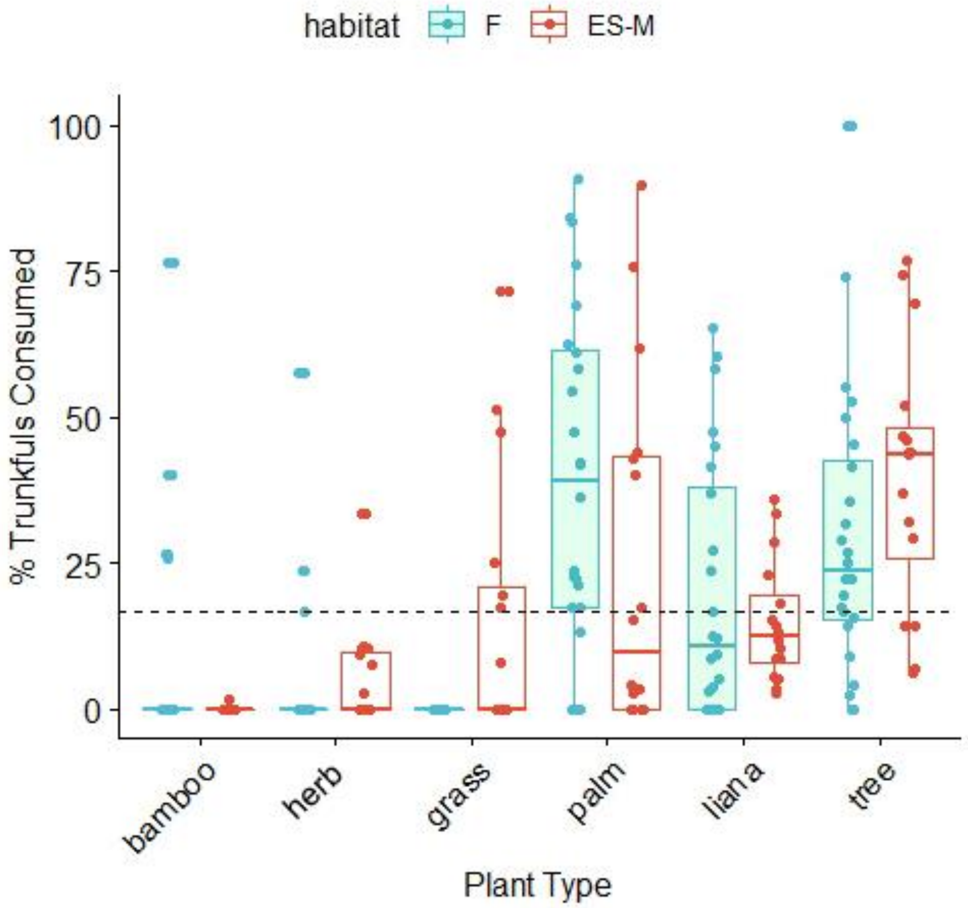


Figure 2.05 Percentage of plants consumed by elephants in different habitats (n= 16 obs. for ES habitat, 24 obs. for F). Shown in graphs: minimum, first quartile, median, third quartile, and maximum values. The dotted line is the observation mean of 16.7%. *zero is assigned to plants not detected.

Apart from plant types, elephants selected certain plant sizes to feed on. Elephants consumed a high quantity of large monocots (34±28%) and large dicot saplings (26±19%) (df=5, x^2=99.3, p= 2.2e^{-16})(N=40 obs.) (Table 2.1–2.3)(Appendix model 2.5, 2.6), especially large palms (23±25%) and large tree saplings (18±16%) (df=15, x^2=173, p< 2.2e^{-16})(N=40 obs.)(Table 2.1)(Appendix model 2.7). In the forest (n=24 obs.), large palms (27±24%), and large tree saplings (17±18%) were eaten in greater proportions, but no grass was consumed (Fig. 2.06,

Table 2.2). In early-successional sites (n=16 obs.), large tree saplings (20±15%) and large palms (16±26%) were eaten more frequently (Fig. 2.06, Table 2.3)(Appendix model 2.8).

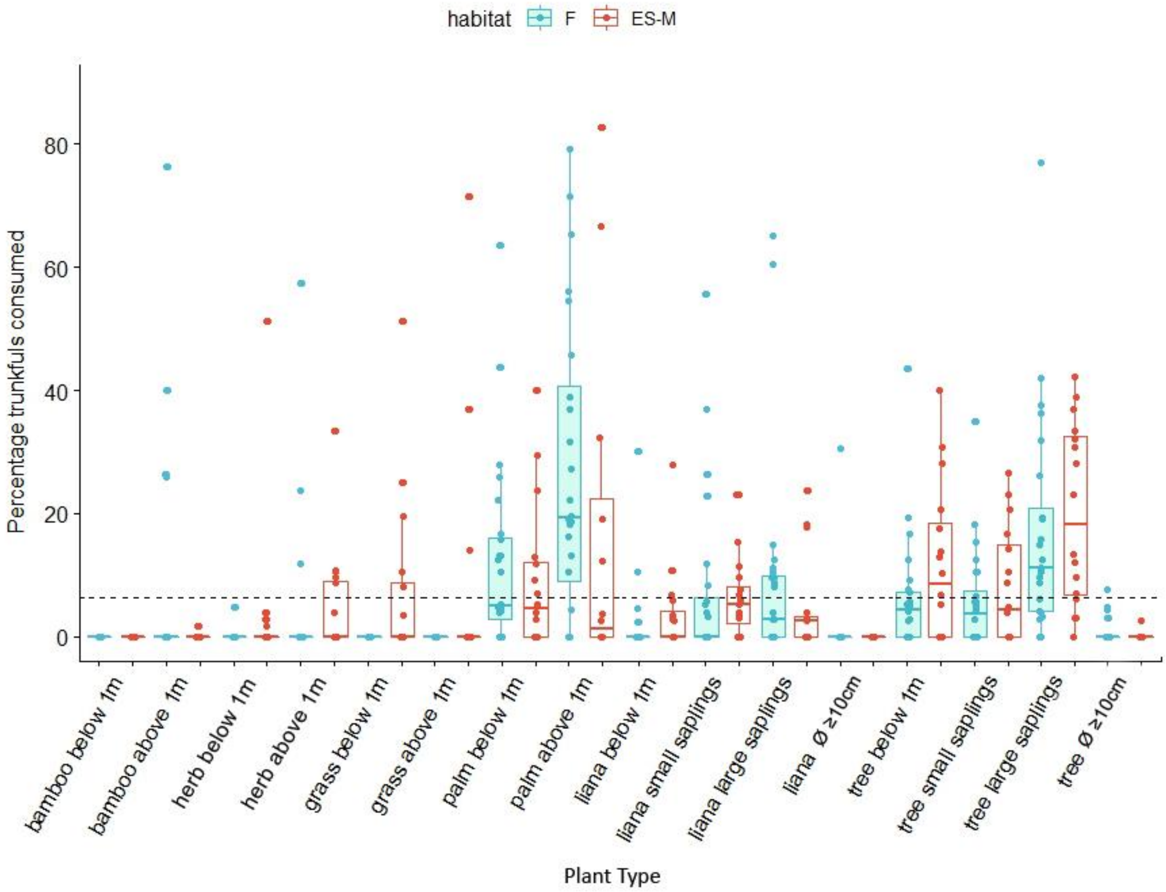


Figure 2.06 Percentage of plant sizes consumed by elephants in different habitats (n= 16 observations for ES-M, 24 observations for F). The dotted line is the observation mean of 16.7%. *zero is assigned to plant not detected.

Individual elephants exhibited different behaviors during feeding. When possible, I incorporated the effects of elephants as random effects in the models. Cherry (age 8), the youngest elephant, for example, consumed a proportionately higher amount of bamboos (25±44%, n=3 obs.) than the average (4±14%, N=40 obs.). Timur (age 43), the oldest elephant, consumed trees proportionately higher (48±20%) than the average (33.7±24%, N=40 obs.). During feeding, while the mahout tried to separate the elephants, Cherry had been observed to stick by older elephants. It is unclear if she was learning what to consume from the older female. For the individual elephant's consumption summary, refer to the appendix (Appendix model 2.1, Fig. A2.4, Table A2).

Table 2.1 (Overall) Elephant diet, food preference, plant availability in habitat, and herbivory impact. Obs.= observations, N=patches number, PR = preference ratio, CI= credible interval. *Plants availability = availability in undisturbed patches. In bold: negative simulations that can be unreliable.

Overall				**Diet**		**Food Preference**			***Plants Availability**			**Herbivory Impact**				
Plant class	**Plant type**	**Plant size**	**Obs.**	**Trunkfuls** Mean±SD	**% diet** Mean%±SD	**N**	**PR** *simulated* ±SD	**CI** (2.5%, 97.5%)	**N**	**Plants availability** Stems ± SD	**% Plants availability** Mean%±SD	**N**	**Impact** *simulated* Mean± SD	**CI** (2.5%, 97.5%)	**N**	**% Plant impacted** (%Plant ± SD)
Monocot	**bamboo**	Small	40	0±0	0±0	-	-	-	-	-	-	-	-	-	-	-
		large	40	2±7	4±14	2	6±35	**-41**,60	16	1±4	1±3	33	NA	NA	2	0±0
	All bamboos		*40*	*2±7*	*4±14*											
	herb	small	40	0±0	0±1	-	-	-	-	-	-	-	-	-	-	-
		large	40	2±5	4±11	9	0.6±1	0,2	16	10±27	6±17	33	4±14	0,9	9	40±49
	All herbs		*40*	*2±5*	*5±11*											
	grass	small	40	1±3	3±9	-	-	-	-	-	-	-	-	-	-	-
		large	40	1±4	3±13	3	2±5	-5, 10	16	3±10	2±6	33	1±2	0,1	3	42±52
	All grasses		*40*	*2±5*	*6±16*											
	palm	small	40	3±4	11±14	-	-	-	-	-	-	-	-	-	-	-
		large	40	6±7	23±25	20	5±5	2,7	16	9±13	7±10	33	4±5	2,6	20	66±45
	All palms		*40*	*9±8*	*34±30*											
		small	40	4±5	14±15	-	-	-	-	-	-	-	-	-	-	-
		large	40	11±11	34±28	27	4±5	2,5	16	23±32	15±22	33	9±15	3,14	27	54±46
	Monocot		*40*	*15±11*	*48±27*											
Dicot	**liana**	seedling	40	1±2	3±7	-	-	-	-	-	-	-	-	-	-	-
		small sapling	40	2±4	7±12	19	1±3	0,3	16	13±18	8±9	33	1±3	0,2	19	21±42
		large sapling	40	2±4	7±14	11	2±4	-1,4	16	10±11	8±10	33	1±2	0,2	11	23±41
		Ø >10 cm	40	0±2	1±5	2	NA	NA	16	0±0	0±0	33	0±1	0,1	2	50±71
	All lianas		*40*	*5±6*	*18±18*	25	1±3	0,2	16	23±21	15±11	33	2±4	1,3	25	44±46
	tree	seedling	40	3±3	8±11	-	-	-	-	-	-	-	-	-	-	-
		small sapling	40	2±2	7±9	31	0±0	0,0	16	43±27	28±18	33	5±8	2,8	31	14±28
		large sapling	40	5±4	18±16	31	1±1	0,1	16	57±34	37±15	33	10±12	6,14	31	27±29
		Ø >10 cm	40	0±0	1±2	6	NA	NA	16	6±6	4±5	33	NA	NA	6	0±0
	All trees		*40*	*9±7*	*34*±24	33	0±1	0.2,1	16	106±50	69±20	33	15±16	9,20	33	20±10
		seedling	40	3±4	11±14	-	-	-	-	-	-	-	-	-	-	-
		small sapling	40	4±5	14±15	32	0±1	0,0	16	57±37	36±23	33	6±9	3,9	32	15±24
		large sapling	40	7±5	26±19	31	1±1	1,1	16	67±40	44±21	33	11±12	7,15	31	26±27
		Ø >10 cm	40	0±2	1±1	8	NA	NA	16	6±6	4±5	33	0±1	0,1	8	13±35
	Dicot		*40*	*14±9*	*52±27*	33	1±1	0.3,1	16	130±62	84±22	33	17±16	11,22	33	20±18
All plants			*40*	*29±10*					16	153±56	NA	33	25±21	18,32	33	25±21

Table 2.2 (Closed forest) Elephant diet, food preference, plant availability in habitat, and herbivory impact. Obs.= observations, n= patches number, PR = preference ratio, CI= credible interval. *Plants availability = availability in undisturbed patches. In bold: negative simulations that can be unreliable.

Closed Forest				**Diet**		**Food Preference**			***Plants Availability**			**Herbivory Impact**				
Plant class	**Plant type**	**Plant size**	**Obs.**	**trunkfuls** Mean±SD	**% diet** Mean%±SD	**n**	**PR** *simulated* ±SD	**CI** (2.5%, 97.5%)	**n**	**Plants availability** Stems ± SD	**% Plants availability** Mean%±SD	**n**	**Impact** *simulated* Mean± SD	**CI** (2.5%, 97.5%)	**n**	**% Plant impacted** (%Plant ± SD)
Monocot (F)	**bamboo**	small	24	0±0	0±0	-	-	-	-	-	-	-	-	-	-	-
		large	24	3±9	7±18	2	5±32	**-48**,51	10	2±5	1±4	20	NA	NA	2	0±0
	All bamboos		*24*	*3±9*	*7±18*											
	herb	small	24	0±0	0±1	-	-	-	-	-	-	-	-	-	-	-
		large	24	2±5	4±13	3	2±3	-3,7	10	8±25	6±15	20	6±17	-2,14	6	87±23
	All herbs		*24*	*2±5*	*4±13*											
	grass	small	24	0±0	0±0	-	-	-	-	-	-	-	-	-	-	-
		large	24	0±0	0±0	2	2±24	**-33**,38	10	0±0	0±0	20	0±2	0,1	1	50±71
	All grasses		*24*	*0±0*	*0±0*											
	palm	small	24	3±5	12±15	-	-	-	-	-	-	-	-	-	-	-
		large	24	7±6	27±24	17	5±5	3,8	10	12±15	9±11	20	6±5	4,9	3	72±41
	All palms		*24*	*10±8*	*39±29*											
		small	24	3±5	12.6±15	-	-	-	-	-	-	-	-	-	-	-
		large	24	11±12	38±29	19	5±5	3,7	10	22±35	16±26	20	12±18	4,20	19	65±42
	Monocot		*24*	*15±13*	*50±30*											
Dicot (F)	**liana**	seedling	42	0±1	2±6	-	-	-	-	-	-	-	-	-	-	-
		small sapling	24	2±4	7±14	10	4±4	-1,3	10	8±13	4±6	20	0±2	0,1	10	10±32
		large sapling	24	3±5	9 ±17	6	2±5	-2,7	10	12±11	9±9	20	1±3	0,2	6	31±52
		Ø >10 cm	24	0±2	1±6	2	NA	NA	10	0±0	0±0	20	NA	NA	2	50±71
	All lianas		*24*	*5±7*	*20±22*	15	1±4	-1,3	10	20±19	13±11	20	2±3	0,3	10	22±41
	tree	seedling	24	2±2	6±10	-	-	-	-	-	-	-	-	-	-	-
		small sapling	24	1±2	6±8	18	NA	NA	10	41±33	24±18	20	4±9	0,8	18	19±34
		large sapling	24	4±3	17±18	20	0±1	0,1	10	65±38	42±15	20	9±13	4,15	20	18±21
		Ø >10 cm	24	0±1	1±2	4	NA	NA	10	6±5	4±4	20	0±0	NA	4	0±0
	All trees		*24*	*7±5*	*30±24*	20	0±0	<0,0	10	11±59	70±24	20	4±9	0,9	20	19±21
		seedling	24	2±3	8±11	-	-	-	-	-	-	-	-	-	-	-
		small sapling	24	3±5	13±17	19	0±1	0,0	10	49±41	28±20	20	5±9	1,9	19	17±29
		large sapling	24	6±5	26±21	20	1±1	0,1	10	77±44	51±21	20	10±13	4,16	20	19±19
		Ø >10 cm	24	0±2	2±6	6	NA	NA	10	6±5	4±4	20	0.4±2	-1,1	6	17±41
	Dicot		*24*	*12±8*	*50±30*	20	0.3±1	0.1,1	10	131±71	83±26	20	15±17	12,23	20	18±18
All plants			*24*	*27±10*					10	153±56	NA	20	27±25	16,38	20	27±24

Table 2.3 (Early Successional) Elephant diet, food preference, plant availability, and impact. Obs.= observations, n= patches number, PR = preference ratio, CI= credible interval. *Plants availability = availability in undisturbed patches. In bold: negative simulations that can be unreliable.

Early successional				**Diet**		**Food Preference**			***Plants Availability**			**Herbivory Impact**				
Plant class	**Plant type**	**Plant size**	**Obs.**	**trunkfuls** Mean±SD	**% diet** Mean%±SD	**n**	**PR** *simulated* ±SD	**CI** (2.5%, 97.5%)	**n**	**Plants availability** Stems ± SD	**% Plants availability** Mean%±SD	**n**	**Impact** *simulated* Mean± SD	**CI** (2.5%, 97.5%)	**n**	**% Plant impacted** (%Plant ± SD)
Monocot (ES)	**bamboo**	small	16	0±0	0±0	-	-	-	-	-	-	-	-	-	-	-
		large	16	0±0	0±0	0	NA	NA	6	0±0	0±0	13	NA	NA	0	NA
	All bamboos		*16*	*0±0*	*0±0*											
	herb	small	16	0±0	1±1	-	-	-	-	-	-	-	-	-	-	-
		large	16	2±3	5±9	6	NA	NA	6	13±33	6±15	13	1±5	-1,4	6	17±41
	All herbs		*16*	*2±3*	*5±9*											
	grass	small	16	3±5	7±14	-	-	-	-	-	-					
		large	16	3±7	8±20	1	NA	NA	6	7±16	4±10	13	1±2	-1,2	1	25±NA
	All grasses		*16*	*5±8*	*15±23*											
	palm	small	16	3±3	9±12	-	-	-	-	-	-	-	-	-	-	-
		large	16	5±8	16±26	3	NA	NA	6	5±8	4±6	13	1±2	-1,2	3	33±58
	All palms		*16*	*8±9*	*25±30*											
		small	16	5±5	17±14	-	-	-	-	-	-	-	-	-	-	-
		large	16	9±9	28±28	8	0±1	0,1	6	25±30	14±14	13	3±5	-1,6	8	28±45
	Monocot		*16*	*14±9*	*45±23*											
Dicots (ES)	**liana**	seedling	16	1±2	4±7	-	-	-	-	-	-	-	-	-	-	-
		small sapling	16	2±2	6±6	9	1±4	-1,4	6	23±22	14±11	13	2±4	0,4	9	33±50
		large sapling	16	1±2	5±8	5	1±4	-2,5	6	7±11	5±10	13	1±2	-1,2	5	10±22
		Ø >10 cm	16	0±0	0±0	0	NA	NA	6	0±0	0±0	13	NA	NA	0	NA
	All lianas		*16*	*4±3*	*15±10*	10	1±2	0,2	6	29±25	19±11	13	2±4	0.1,5	10	20±33
	tree	seedling	16	4±4	12±13	-	-	-	-	-	-	-	-	-	-	-
		small sapling	16	3±3	8±9	13	0.3±1	0,1	6	48±15	35±17	13	5±8	-1,2	13	7±14
		large sapling	16	7±5	20±15	11	2±1	1,3	6	44±24	28±10	13	12±12	5,18	11	41±35
		Ø >10 cm	16	0±0	0±1	2	NA	NA	6	7±8	5±7	13	NA	NA	2	0±0
	All trees		*16*	*13±9*	*40±22*	13	1±1	0,1	6	98±29	68±12	13	17±15	8,25	13	21±19
		seedling	16	5±5	15±17	-	-	-	-	-	-	-	-	-	-	-
		small sapling	16	5±4	14±11	13	0±1	0,1	6	48±15	15±35	13	7±8	2,11	13	11±14
		large sapling	16	8±5	28±28	11	2±1	1,2	6	44±24	24±28	13	12±12	5,20	11	38±35
		Ø >10 cm	16	0±0	0±0	2	NA	NA	6	7±8	8±5	13	NA	NA	2	0±0
	Dicot		*16*	*17±9*	*55±23*	13	1±1	1,1	6	127±47	86 ±14	13	19±16	10,28	13	22±17
All plants			*16*	*32±10*					6	153±62	NA	13	21±16	13,31	13	21±15

Availability of plants in the habitat – Only plants 1m or taller were measured (N=16). By stems, 100 m^{-2}, closed forest had an average of 153±56 stems 100 m^{-2} (n=10 undisturbed circular patches)(Table 2.2), and early-succession forests had about 153±62 stems 100 m^{-2} (n=6 undisturbed patches)(Table 2.3). Trees were more abundant than other plant types in both closed forests (70±24%) and shifting agriculture influenced early successional habitats (68±12%). Palms (9±11%) were more abundant in the forest than in early-successional (4±6%) habitats (Table 2.2 and 2.3). By plant sizes, there were more large tree saplings in the forest (42±15%) than in early-successional habitats (28±10%) (Table 2.1; Fig. 2.07).

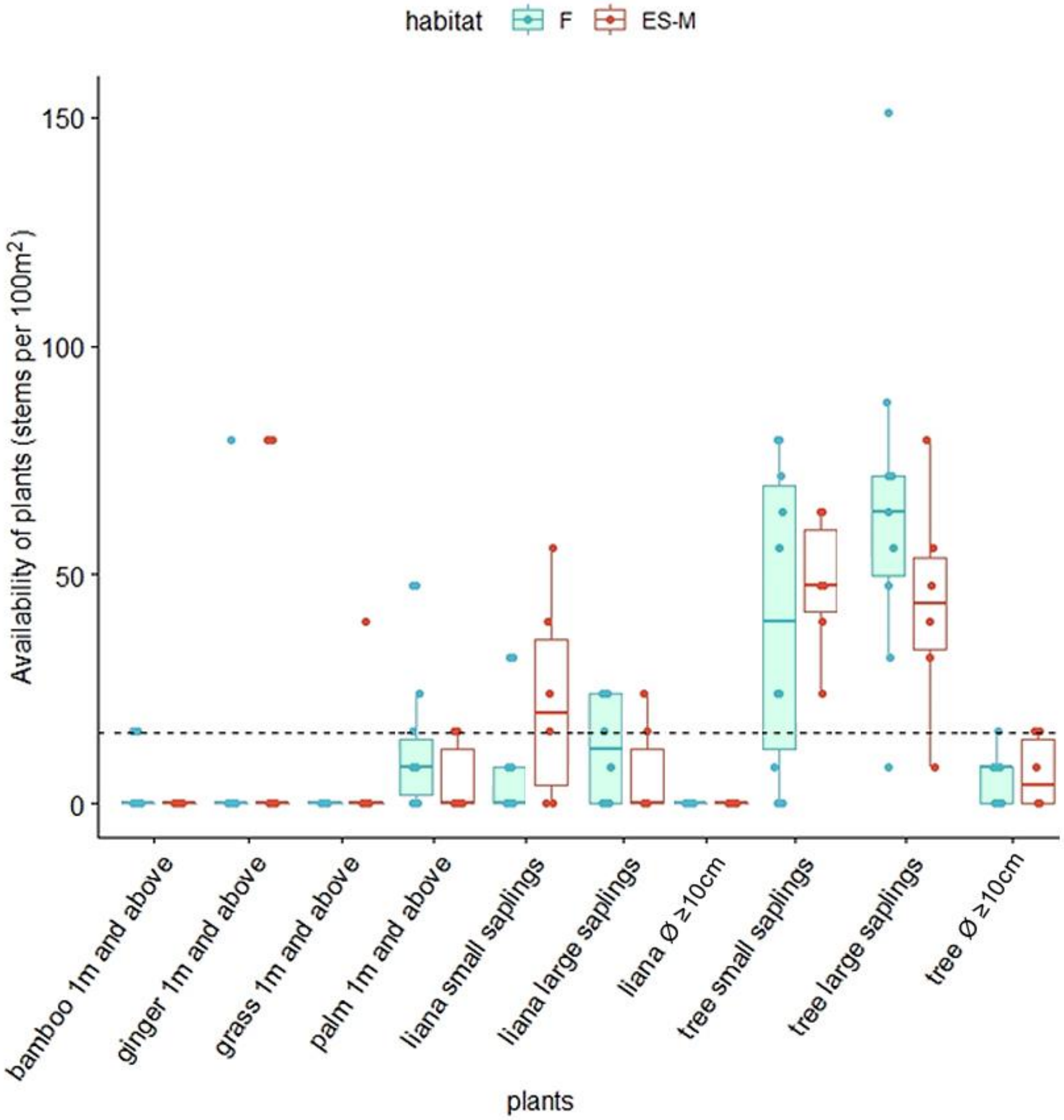


Figure 2.07 Availability of plants above 1m in unforaged patches (forest n=10, early-successional n=6).

Food preferences – Overall, I found elephants strongly preferred palms (PR*simulated* = 5±5, credible interval CI = 2–7, 0%< PR 1<100%), and avoided trees (PR*simulated* = 0±1, CI = 0–1, 100%< PR 1<0%) (Fig. 2.08). In the forest, elephants strongly preferred large palms (PR*simulated* = 5±5, CI = 3–8, 0%< PR 1<100%), and avoided large tree saplings (PR*simulated* = 0±1, CI = 0–1, 100%<PR 1<0%) (Fig. 2.09). In early-successional habitats, large tree saplings (PR*simulated*=2±1, CI =1–3, 7%<PR 1<93%) were preferred (Table 2.1, Fig. 2.09). The sample sizes of monocot plants were too small to provide good inference for preference, as shown by simulated negative credible intervals (Table 2.1–2.3).

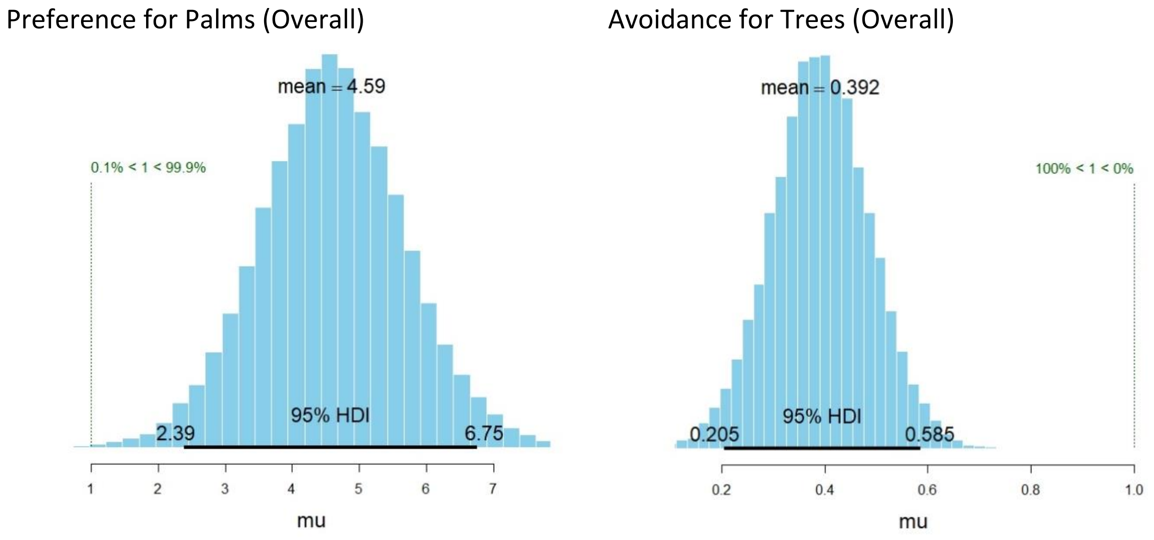


Figure 2.08 Probability density functions of elephant's preference for palms (left): credible interval, CI range (2.4–6.8). 0.1%< PR 1<99.9% infers a probability of 0.99 of being preferred. Probability density functions of elephant's avoidance for trees (right): CI range (0.2–0.6).

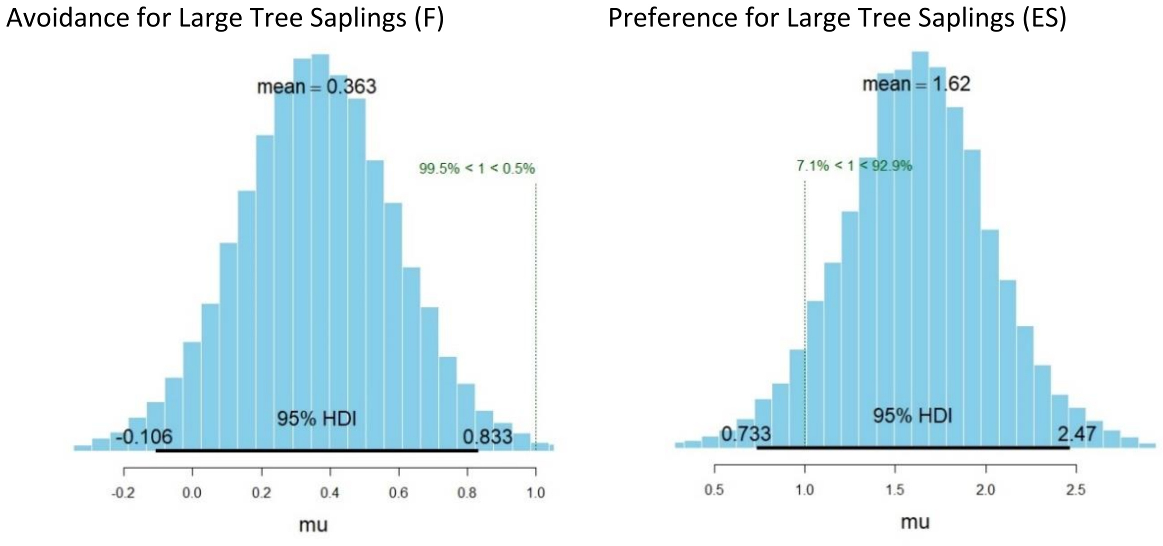


Figure 2.09 Probability density function of elephant's avoidance for large tree saplings in the forest (left): CI range (-0.1–0.8). The probability density function of the elephant's preference for large tree saplings in early-successional habitats (right): CI range (0.2–0.6).

Herbivory Impact of Elephants – I included only plants that were debarked, broken at the main stem, pushed-over, or uprooted by elephants as impacts (damaged). Branch breakage and leaf stripping were excluded. Due to the under-sampling of some plant types, impacts on stems were simulated with Bayesian computation from measurements taken from the field (refer to Statistical Analyses: Preference and Impacts). Precautions need to be taken in interpreting these results, where negative CI numbers indicate unreliable estimations (Table 2.1).

Closed forests had an average of 153±56 stems 100m^{-2} (n=10 undisturbed patches). The mean impact was 27.4±24.7 stems 100 m^{-2} (95% credible interval, CI =16–38) (n=20). Plants below 1m, including small monocots, were not sampled. Measurements from foraged patches (n=20 patches) revealed a high proportion of large monocots were impacted, i.e. about 65±42% out of 22±35 available stems. Large herbs (87±23% of 8±25 stems), large palms (72±41% of 12±15 stems), and small liana saplings (31±52% of 12±11 stems) were extensively damaged (Fig. 2.10 and 2.11). Although the intensity of damage on trees was lower, the total number of stems damaged was highest. Both small tree saplings (19±34% of 41±33 stems) and large tree saplings (18±21% of 65±38 stems) added up to around 13 tree saplings, as compared to 6 palms and 6 herbs damaged (Fig. 2.10 and 2.11).

Early-successional habitats had an average of 153±62 stems 100 m^{-2} (n=6 undisturbed patches). In foraged patches (N=13), the mean impact recorded was 21±16 stems 100 m^{2} (95% credible interval=12.6,30.6). Large tree saplings (41±35% of 44±24 stems), small liana saplings (33±50% of 23±22 stems), and palms (33±58 of 4±6 stems) were commonly damaged (Fig. 2.10 and 2.11).

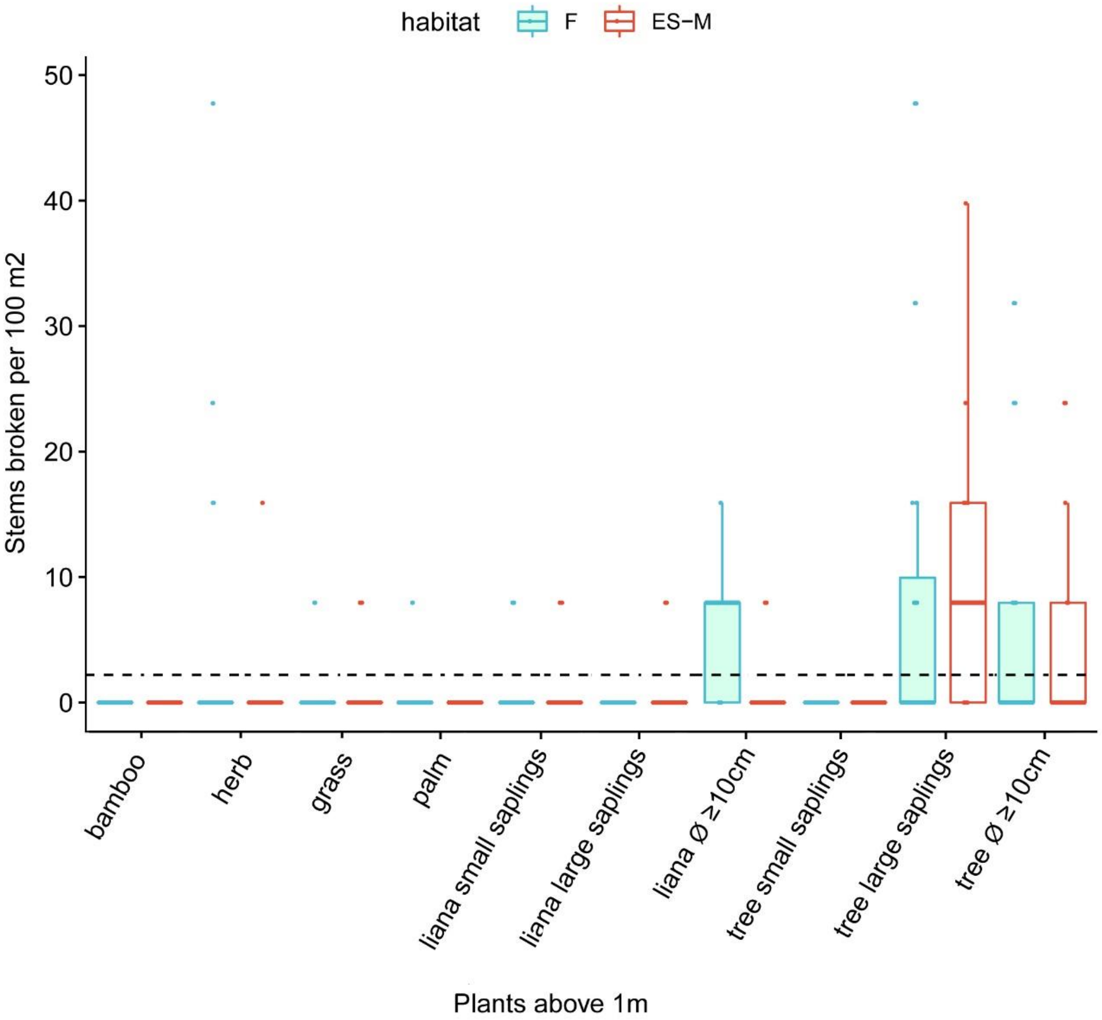


Figure 2.10 Impact of plants above 1m in foraged patches(forest n=10, early-successional n=6)

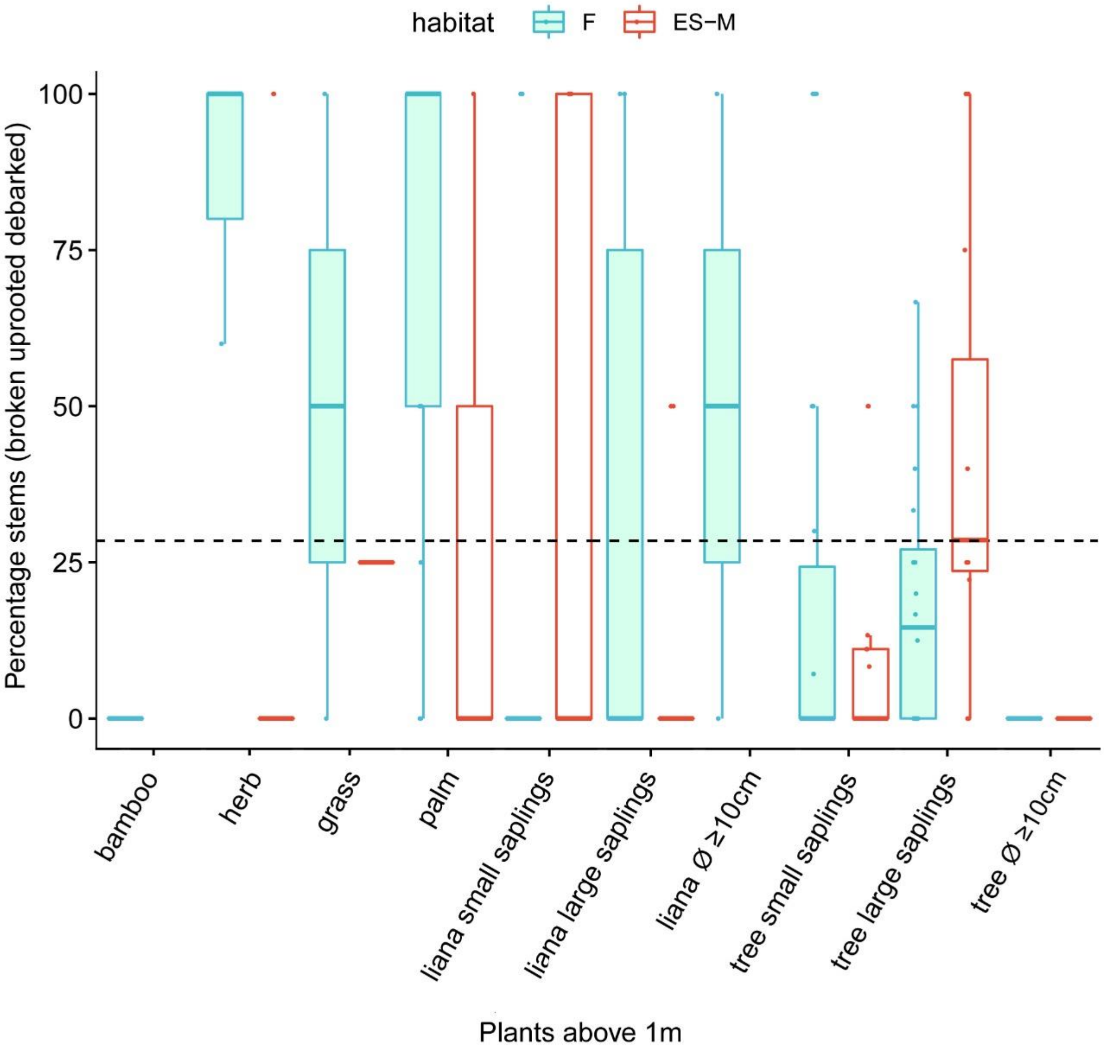


Figure 2.11 Percentage of stems broken, uprooted, and debarked in the forest and early-successional habitat and trees (n= 1 debarked, 176 stem breakage, 19 uprooted)

Taking measurements from all tagged plants, the average diameter of dicot stems broken by Asian elephants was 1.7±1.1 cm (range 0.2–7.1 cm, n=190 stems). Trees were broken at an average diameter of 1.7±1.1 cm (range = 0.2–7.1 cm, n=176 stems; Fig. 6) and at a mean height of 1.1±0.5 m (range = 0.1–2.8 m, n=161 stems). Lianas were broken at a mean diameter of 1.4±1.1 cm (range = 0.2–3.5 cm, n=14).

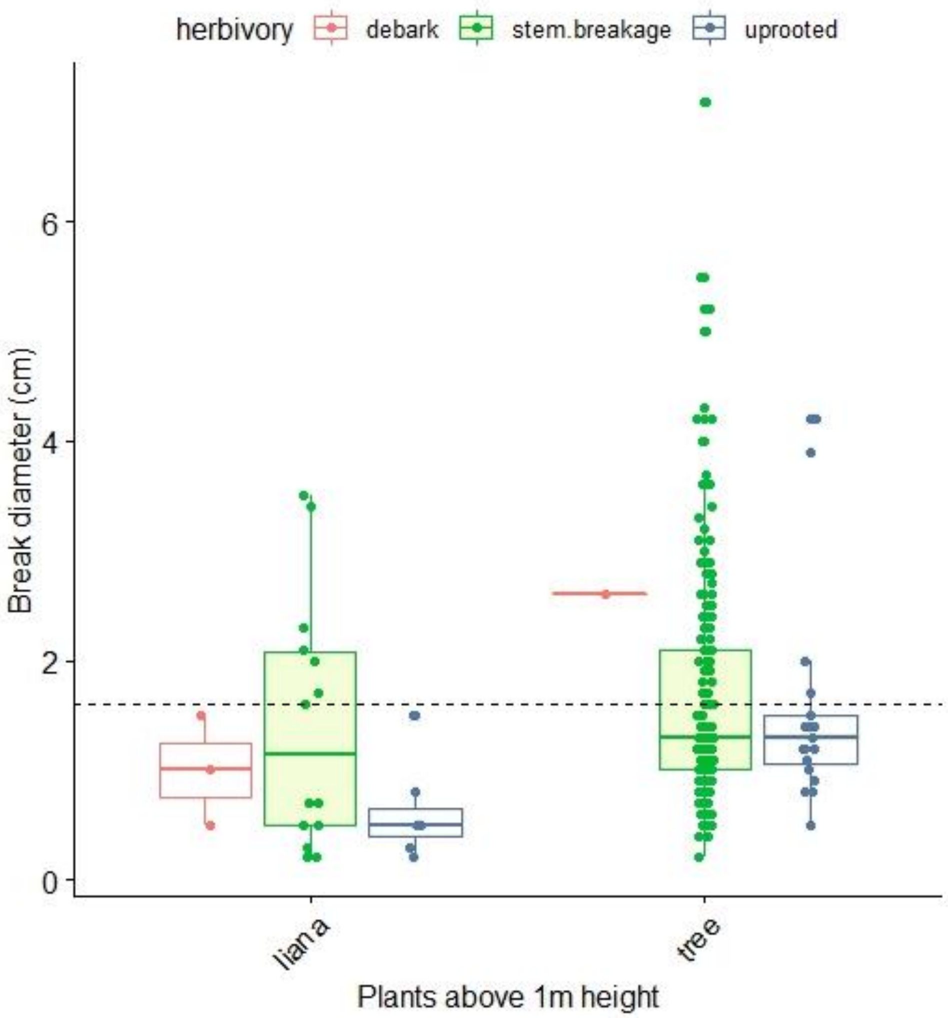


Figure 2.12 Break diameter of lianas (n=3 debarked, 14 stem breakage, 7 uprooted)

Apart from creating strong impacts – i.e., uprooting, breaking, or debarking stems – elephants also broke branches and stripped leaves. Many of these herbivory damages include stems that were accidentally broken or were rejected while feeding. The proportional herbivory damage gathered from direct observations is shown in Fig. 2.13. Refer to Fig. A2.5 for relative herbivory damage in closed forest, and Fig. A2.6 to herbivory damage in early successional habitats. Damages recorded from direct observations and foraged plots are different. From foraged plots, it was difficult to keep track of uprooted and leaf-stripped plants. Refer to Fig. A2.7 for herbivory damage gathered from patches. Plants below 1m were not counted.

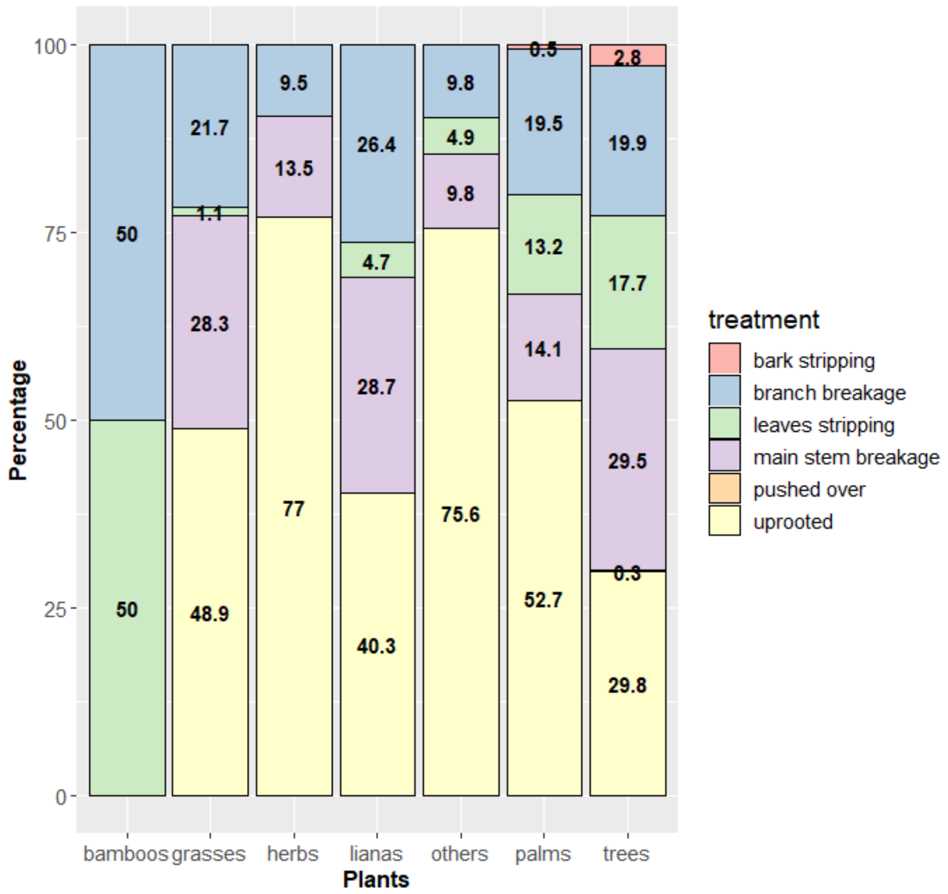


Figure 2.13 Proportional herbivory damage on plants through direct observations.

DISCUSSION

The herbivory influence of forest-dwelling Asian elephants (*Elephas maximus*) in tropical rain forests is under-studied. In a previous study, my collaborators and I speculated that selective browsing by elephants could result in lower density and diversity of saplings and palms in elephant-present forests than in elephant-absent forests. Here, we followed up with direct observations of elephant feeding to determine if selective browsing (plant type and plant size) is evident by identifying both the principal and preferred food of elephants (Petrides, 1975). The interplay of both browsing trends could potentially lead to a general reduction of browsed plants in the system. I also discuss the importance of elephant browsing to the Sundaic dipterocarp rainforest system, and the implications associated with the findings.

Elephants' Diet, Selective Browsing and Impact on Stems

The overall diet composition recorded in the studied elephants provided a useful generalization of an Asian elephant's diet and preferences. I found Asian elephants consumed similar amounts of monocots and dicots. Their diet was dominated by trees and palms that each formed nearly 34% of the diet. Palms were also one of the most preferred foods, surpassed only by bamboo. However, the sample sizes of bamboos (n=2 patches) and grasses (n=3) were too small to provide conclusive inferences.

Palms are very important food items for Asian elephants in Malaysia (Olivier 1978, this study) and sustained severe impacts from their foraging. The importance of woody species in the diet of elephants and the impacts they can have on these growth forms have not been widely emphasized within the literature. To understand the effects of elephant browsing, I assessed elephants' feeding and impacts relevant to a habitat type. I found different feeding intensity and preferences within the different habitat types. In the closed forest, palms were both the principal and preferred food of elephants. Impacts (72% with main-stems damaged or uprooted) on palms were highest, at about 6 stems 100 m^{-2} in foraged patches. From direct observations, about 53% of palms eaten were uprooted. With high consumption, high preference, high impact (broken and uprooted), and low availability of palms in closed-forest systems, it is likely that the density of palms in the forest could be suppressed by long-term foraging by Asian elephants.

Elephants are generalistic herbivores that eat a wide range of foods (Sukumar, 2006; Campos-Arceiz et al., 2008) and this study found that trees were as highly consumed as palms. Within trees, size-selection feeding was most prominent for tree saplings. In the habitat patches, a quarter of the plants sustained damage, and tree saplings represented more than half of the damages incurred. The average diameter of stems broken by elephants was small – at around 1.7 cm. In the forest, around a third of the plants in foraged patches sustained damages, and more than half of the stems damaged were tree saplings. From direct observations, about 30% of stems consumed by elephants were uprooted. Consistent high consumption of tree saplings could lead to a potential long-term reduction of stem densities.

In early-successional forest gaps, I had expected a higher consumption of monocots by Asian elephants, as several studies indicated a high amount of grasses consumed by Asian elephants in grassland habitats (Sukumar 1990; English et al., 2014). Instead, Asian elephants fed on high amounts of trees (40% of diet make-up) primarily represented by Euphorbiaceae (e.g., *Macaranga* and *Mallotus* spp.) as compared to grasses (15.0%). Here, high biomass production and competition for light favour broad-leaved pioneer species with a low root/ shoot ratio. These fast-growing pioneer species have fewer defenses against herbivores than slow-growing forest species (Fraser & Grime, 2000). In contrast, to browse, grasses are low-quality food that are more fibrous and abrasive (Osborn, 2005; Damuth & Janis, 2011; Venter et al., 2019). Ruminants are foregut fermenters with a long digestive passage time that allows for high consumption of grasses as food. Unlike ruminants, elephants are hindgut fermenters with a higher volume of masticatory musculature that could process food less selectively than most ruminants (Janis, 2004; Clauss et al., 2009). The adaptation to a mixed-browser diet is also reflected in the molar morphology of elephants — having 'multilophed' parallel ridges of enamel as several rodents and wombats (Janis, 1998; 2004). Specialized ruminants and perissodactyls have complex 'plagiolophodont' with cross-linked occlusal enamel surfaces (Janis, 1998; 2004).

The results showed that elephants preferred large saplings in early successional habitats. Asian elephants may have preferred feeding on small monocots in early-successional habitats, but the method that we employed was unable to detect this preference. An artifact of grass availability may have resulted as plants below 1 m were not sampled. Grass may also be of low availability because gaps created by slash-and-burn practices – which favour grass growth – were small. A biomass approach would serve to answer this better.

Asian elephants as Determinants for Forest Structures and Composition

African forest elephants are considered to be powerful filters on the tree recruitment process by intensively damaging tree saplings (Terborgh et al. 2015; 2016). From this study, I was unable to confirm this filtering ability for Asian elephants. I found similarities in the stem sizes broken by Asian elephants (0.2 to 7 cm; mean of 1.7 cm) and African forest elephants (2 to 6 cm; Struhsaker et a., 1996; Sheil & Salim, 2004). The majority of stems broken by both elephant species were below 4 cm. Large stems were more frequently pushed over.

In this study, size-selective browsing of small saplings by Asian elephants supported the possibility of reduced stem densities in rainforest over long-term feeding, thus affecting forest structure. However, by simulating elephant breaks through manually cut saplings in Belum, Terborgh et al. (unpubl.) found around 90% of the cut stems resprouted. High recovery rates indicated that the possibility of the influence of elephant browsing on forest structure is likely low. In Peninsular Malaysia, the effect of pigs on understorey woody vegetation is high. Pigs harvest stems to build nests and uproot plants for food. The added effects of wild boars may reduce stem recruitment up to three times in wild boars utilised areas (Ickes at al., 2003).

The filtering effect may also depend on several other factors that are unexplored in studies of rainforest Asian elephants. For example, the density and diversity of saplings corresponding to the density of elephants (Terborgh et al. 2015; 2016), the foraging strategies of elephants, and how recursion relates to the long-term recovery of plants (e.g., English et al., 2014). Ecological factors, independent of elephant presence, could impose more substantial effects on forest structure and composition than elephant browsing. In Africa, reduced stem densities by forest elephants were linked to changes in competition for light, water, and space among trees that subsequently led to the growth of fewer and larger trees of high wood density, boosting aboveground carbon stocks (Berzaghi et al., 2019). In Malaysia, trees from the Dipterocarpaceae are soil-specialists that are exceptionally adapted to different soil types (Davies et al., 2003; Palmiotto et al., 2004), and dominate both canopy cover, as well as basal forest area (Corlett & Primack, 2005; Frechette, 2014). Elephants fed on a large number of woody saplings. Are dipterocarps dominant because of how well they adapt to the soil, or because Asian elephants and perhaps other now-extinct megafauna avoid consuming these species? And if this theory is true, should we be seeing less of the avoided species in the younger trees in Sarawak or Western Sabah where no elephants are found? These uncertainties remained unanswered. Extensive studies considering both abiotic and biotic processes are needed to provide us with the bigger picture of the drivers of Sundaic forest structure.

Importance of Asian Elephants and Local Indigenous Practices

The indigenous people have lived alongside Asian elephants for 55,000 years, sharing a considerable degree of coexistence in the landscape (Lim, 2020). The relationship between large animals and indigenous practices is important to the forest but is difficult to quantify. For example, the maintenance of fruit gardens was found to be feeding hotspots for animals in the Krau wildlife reserve, Malaysia (Moore et al., 2016). The early-successional habitats in this study were mainly sites characteristic of the slash-and-burn practice by the Orang Asli. The abandoned sites leftover from small-scale clearings by the Orang Asli encourage the growth of pioneer species. These gaps could serve as herbivores feeding sites. As supported by this study, elephants fed on a high amount of tree saplings from the *Macaranga* and *Mallotus* spp.

In Krau, the indigenous people of the Cheq Wong tribe practice crop rotation. In such practices, intermittent planting requires plots to be left to rest. During this period, animals may roam freely in these clearings. The size of gaps has a huge influence on nutrient loss through leaching. In large gaps associated with logging, up to 50% of nutrients can be lost through leaching (Brouwer & Riezebos, 1998). When nutrient-poor forests are cleared for agricultural purposes, the systems quickly lose their productive potential (Jordan & Herrera, 1981; Smithson & Giller, 2002). Unlike sites left-over from large-scale loggings, gaps created by Orang Ali for shifting agricultural practices are relatively small, thus limiting the amount of leaching. Once planting takes place in these patches, the Orang Asli will attempt to guard their sites from elephants. Thus limiting the damage elephants can potentially cause in gaps over longer terms. With the presence of elephants in the forests, indigenous practices are also limited. In the Amazon forests where no megaherbivores are present, such adverse effects have been observed with the expansion of unsustainable practices (Steinberg, 2010).

Herbivores, especially megaherbivores such as elephants could play important roles in regulating the nutrient availability of the Dipterocarp rainforests system. Firstly, by improving soil fertility. Secondly, by indirectly enhancing the availability of palatable foliage for other herbivores through defoliation. Tropical forests are more nutrient-poor than temperate forests. Under disturbed conditions, the nutrient-poor ecosystem is unable to maintain its productivity (Jordan & Herrera, 1981; Brouwer & Riezebos, 1998). Decomposition involves a fast cycling of low molecular weight carbon (e.g. microbial residue) and a slow-cycling of recalcitrant molecules (e.g. cells of plant, fungi and arthropod exoskeleton) (Coleman et al., 1983). Large herbivores such as elephants can help maintain this productivity by fertilizing soils with nitrogen in the form of dung to the humus and root layer of the mineral soil. Without large animals, nitrogen management is required but limited with methods such as legume rotations. Over time, the system easily becomes nutrient-depleted (Smithson & Giller, 2002).

The relationship between large herbivores and plants has been demonstrated in several studies (e.g., Cumming, 1982; Owen-Smith, 1989; Malhi et al., 2015; Terborgh et al., 2015; Ripple et al., 2016). In addition to soil fertilising, browsing and grazing by herbivores affect plant physiology, regulating mineral uptakes, and creating strong sinks in the residual plant tissues. As leaf nutrient concentration and specific root uptake of nutrients increases, the growth rates of plants increase. This process generates regrowth flushes that enhance leaf production two to threefold, providing quality forage to herbivores. In this way, grazing creates a positive feedback loop through the resultant improvement of nutrient availability (Ruess, 1984; McNaughton and Chapin 1985; Teague, 1985; Turner, 2004). Yet to be tested in the dipterocarp rainforest, the benefits of large animal-mediated defoliation can be further explored.

This study showed Asian elephant browsing caused considerable damage to young woody stems. In dipterocarp forests, leaves and barks of trees have high concentrations of phenolic compounds such as tannins that help plants defend against herbivores. Mature leaves are high in fiber and protein and are unpalatable to most herbivores (Turner, 2004). A large amount of energy that is available in the system is thus not utilizable for most animals. Elephants do not appear to be highly restrained by phenolic compounds in young trees. Stem breaking by elephants, thus, could play important roles in regulating the nutrient availability of the

Dipterocarp rainforests system. Without animals such as elephants and wild boars breaking stems (Ickes et al., 2003), less foliage would be available to smaller herbivores. Nutrient availability is also limited. Gaps created by agricultural practices and logging could have detrimental effects on nutrient loss, threatening the overall resilience of the system.

In a previous study, we found a lower density of tree saplings and palms in Belum, where elephants are present, as compared to Krau which was void of elephants since 1993. However, the densities of seedlings (plants below 1m) between both sites were similar. Following the exclusion of elephants, wild boars are remnant large animals with the potential for breaking large numbers of woody plants. As wild boars do not cause extensive damage to palms, palms were abundant in Krau. In contrast, palms were very scarce in Belum. The high preference of elephants for eating palms might have eliminated a large proportion of young palms from the forest. It is uncertain if the difference in tree saplings density could be largely due to elephant browsing or stem harvesting by wild boars. Further studies comparing the density of wild boars in both forests, as well as the effects of uprooting by both species could allow us to have a clearer understanding of their effects on forest structure.

CONCLUSION

The diet of Asian elephants comprises a high amount of both monocots and dicots in the Malaysian rainforest system. In the closed-canopy forest, palms are both their principal and preferred food. Asian elephants are likely to contribute to reduced palm densities in a forest where palms are subjected to persistent feeding. This is consistent with our previous observations of lower palm density in an elephant-present forest, Belum, as compared to Krau, where elephants are absent. As mixed-feeders, elephants also consumed a large number of woody plants. Amongst trees, elephants selectively browsed for tree saplings. Tree saplings in Krau were also less dense than Belum. Although elephants damage a large number of tree saplings, most saplings have high recovery abilities. While reduced palm density is more obviously linked to elephant herbivory, reduced sapling density could be linked to both elephant herbivory and stem harvesting by wild boars. Stem breaking by large herbivores creates a positive feedback loop for the nutrient cycles and could be important for producing palatable foliage for other animals in the dipterocarp rainforests. Forest gaps created by the shifting agricultural practices of local indigenous people may also create healthy habitats for herbivores to feed. The relationship of large herbivores, the indigenous people, and the productivity of the system can be further explored.

APPENDIX

Chapter Two: Diet Models

Model 2.1: Plant class (monocots and dicots)
Comparing equations:
2.1a: mouth ~ 1 + (1 | elephant)
2.1b: mouth ~ Plant class + (1 | elephant)

Equation	Df	AIC	Log likelihood	deviance	Chisq	Df	Pr(>Chisq)
2.1a	3	598.05	-296.02	592.05			
2.1b	4	600.01	-296.01	592.01	0.0334	1	0.855

Model 2.2: Plant class (monocots and dicots) * habitat
Comparing equations:
2.2a: mouth ~ Plant class + habitat + (1 | elephant)
2.2b: mouth ~ Plant class * habitat + (1 | elephant)

Equation	Df	AIC	Log likelihood	deviance	Chisq	Df	Pr(>Chisq)
2.2a	5	600.78	-295.39	590.78			
2.2b	6	601.19	-294.60	589.19	1.59	1	0.2073

Model 2.3: Plant type (bamboo, herb, grass, palm, liana, tree)
Comparing equations:
2.3a: mouth ~ 1 + (1 | elephant)
2.3b: mouth ~ Plant type + (1 | elephant)

Equation	Df	AIC	Log likelihood	deviance	Chisq	Df	Pr(>Chisq)
2.3a	3	1369.0	-681.51	1363.0			
2.3b	8	1310.1	-647.07	1294.1	68.867	5	$1.763e^{-13}$

Model 2.4: Plant type (bamboo, herb, grass, palm, liana, tree) * habitat
Comparing equations:
2.4a: mouth ~ Plant type + habitat + (1 | elephant)
2.4b: mouth ~ Plant type * habitat + (1 | elephant)

Equation	Df	AIC	Log likelihood	deviance	Chisq	Df	Pr(>Chisq)
2.4a	9	1311.5	-646.77	1293.5			
2.4b	14	1279.1	-625.56	1251.1	42.412	5	$4.861e^{-8}$

Model 2.5: Plant class sizes (small monocots, large monocots, dicot seedlings, small dicot saplings, large dicot saplings, dicots diameter, Ø >10 cm)

Comparing equations:

2.3a: mouth ~ 1 + (1 | elephant)

2.3b: mouth ~ Plant type + (1 | elephant)

Equation	Df	AIC	Log likelihood	deviance	Chisq	Df	Pr(>Chisq)
2.5a	3	1364.8	-679.38	1358.8			
2.5b	8	1275.4	-629.71	1259.4	99.346	5	$<2.2e^{-16}$

Model 2.6: Plant class sizes (small monocots, large monocots, dicot seedlings, small dicot saplings, large dicot saplings, dicots Ø > 10 cm) * habitat

Comparing equations:

2.6a: mouth ~ Plant class sizes + habitat

2.6b: mouth ~ Plant class sizes * habitat

Equation	Theta	Resid. df	2 x log likelihood	Df	LR stat	Pr(>Chisq)
2.6a	0.8647938	233	-1159.403			
2.6b	1.496322	228	-1145.234	5	14.16867	0.01457274

Model 2.7: Plant type sizes (small bamboo, large bamboo, small herb, large herb, small grass, large grass, small palm, large palms, liana seedlings, small liana saplings, large liana saplings, lianas Ø >10 cm, tree seedlings, small tree saplings, large tree saplings, trees Ø >10 cm)

Equations:

2.7: mouth ~ Plant class sizes

Equation	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chisq)
Null			639	635.58	
2.7	15	173.03	624	462.55	$< 2.2e^{-16}$

Model 2.8: Plant type sizes (small bamboo, large bamboo, small herb, large herb, small grass, large grass, small palm, large palms, liana seedlings, small liana saplings, large liana saplings, lianas Ø >10 cm, tree seedlings, small tree saplings, large tree saplings, trees Ø > 10 cm)* habitat

Comparing equations:

2.4a: mouth ~ Plant class sizes + habitat

2.4b: mouth ~ Plant class sizes * habitat

Equation	Theta	Resid. df	2 x log likelihood	Df	LR stat	Pr(>Chisq)
2.4a	0.3014369	623	-1810.220			
2.4b	0.3804263	608	-1724.277	15	85.94286	$5.630052e^{-12}$

Table A2.1 Mean percentage of plants consumed by different elephant individual. N Obs. = number of observations.

Elephant	**Age**	**N Obs.**	**n (Habitat)**	**Plants**	**% consumed (mean±SD)**
Cherry	8	3	2 F, 1 ES-M	bamboo	25 ± 44
				herb	11± 12
				grass	16 ± 27
				palm	14 ± 24
				liana	4± 3
				tree	30 ± 27
mean					*31± 21*
Indah	20	7	6 F, 1 ES-M	bamboo	0
				herb	1 ± 4
				grass	0
				palm	49± 23
				liana	27 ± 13
				tree	23 ± 15
mean					*20 ± 3*
Sanum	12	14	8 F, 6 ES-M	bamboo	2 ± 7
				herb	3 ± 5
				grass	5 ± 15
				palm	35 ± 36
				liana	15 ± 18
				tree	39 ± 29
mean					*29 ± 8*
Siti	37	13	6 F, 7 ES-M	bamboo	3 ± 11
				herb	8 ± 18
				grass	7 ± 20
				palm	28 ± 27
				liana	23 ± 21
				tree	31 ± 21
mean					*33 ± 11*
Timur	43	3	2 F, 1 ES-M	bamboo	9 ± 15
				herb	1 ± 2
				grass	6 ± 11
				palm	33 ± 27
				liana	3 ± 3
				tree	48 ± 20
mean					*30 ± 7*
Total		***40***	***24 F, 16 ES-M***		

***Additional discussion on statistical methods applied for preference* – Table A2.2** presents an alternate solution to calculate preference ratio. This result is only presented for comparison, not for inference. Here, I use relative use from the diet of elephants through direct observations (RUa), and relative availability from unforaged patches to derive with preference ratio (PR$_a$). I compared this to the preference ratio (PR$_b$) using relative use of "eaten" stems from foraged patches (RUa). From PR$_a$, I see overall preference in most monocots. This is largely due to the over-represented trees, in which non-food plants were not filtered. The advantage of using this method is that the true elephant diet ca be used to account for preference. In this method, synchronizing the units of representation is commonly practiced. For example, by converting availability in the forest to mouthful (as in Olivier, 1978), or by taking plant stems as the unit (as in English, 2014). In this method, it will be ideal to include only foodplants in the assessment. This method, however, do not that into account variation across different patches, resulting in preference ratios being highly skewed.

Table A2.2 Preference ratios (PR$_a$) derived from plants eaten (diet, RU$_a$) and relative availability of plants, RA$_1$ from unforaged patches; and preference ratio (PR$_b$) derived from plants used (RU$_b$) from foraged plants.

		By mouthful		*By stems*		
Plant type	**Habitat type**	**RU$_a$** (from diet)	**RU$_b$** (foraged patches)	**RA$_1$** (unforaged patches)	**PR$_a$** (RU$_a$/RA$_1$)	**PR$_b$** (RU$_b$/RA$_1$)
Bamboo	overall	0.04	0.5	0.01	4.0	50.0
Herb	overall	0.05	0.2	0.06	0.8	3.3
Grass	overall	0.06	0.5	0.02	3.0	25.0
Palm	overall	0.34	0.5	0.07	4.9	7.1
Liana	overall	0.18	0.3	0.15	1.2	2.0
Tree	overall	0.34	0.3	0.69	0.5	0.4
Bamboo	Forest	0.07	0.5	0.01	7.0	50.0
Herb	Forest	0.04	0.5	0.06	0.7	8.3
Grass	Forest	0	0.3	0.001	0.0	300.0
Palm	Forest	0.39	0.5	0.09	4.3	5.6
Liana	Forest	0.2	0.2	0.13	1.5	1.5
Tree	Forest	0.3	0.1	0.7	0.4	0.1
Bamboo	ES	0.01	0.001	0.001	10.0	1.0
Herb	ES	0.05	0	0.06	0.8	0.0
Grass	ES	0.15	0.001	0.04	3.8	0.0
Palm	ES	0.25	0	0.04	6.3	0.0
Liana	ES	0.15	0.2	0.19	0.8	1.1
Tree	ES	0.4	0.6	0.68	0.6	0.9

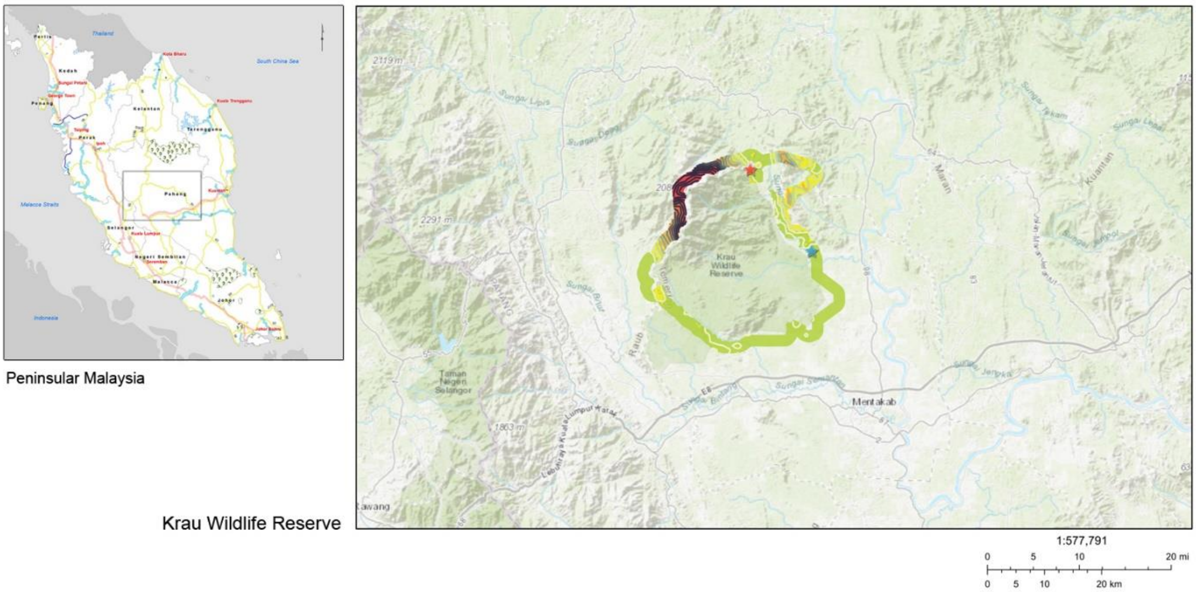


Figure A2.1 Map of Krau Wildlife Reserve (Source: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS), Peninsular Malaysia.

Figure A2.2 Mahouts (left) and our chief guide, Ali G (right) from the Elephant Capture and Translocation Unit, Department of Wildlife and National Parks (DWNP).

Asian Elephant Herbivory

Figure 2.3a Elephant stripping leaves of large sapling (left) and field assistant, Param investigating a small stripped sapling (right).

Figure 2.3b Elephant breaking a large sapling to obtain the leaves (left). A plant broken at the main stem (right).

Figure 2.3c Elephant debarking a large sapling (left) and a debarked stem (right).

Figure 2.3d Elephant eating roots of a large sapling (left) and an uprooted stem (right).

Figure 2.3e Elephant pushing over a tree.

Figure 2.3f Elephant eating a small liana (left) and large liana sapling (middle). Liana stem broken by elephant (right).

Figure 2.3g Elephant eating palm (left) and uprooted palm (right).

Figure 2.3h Elephant eating bamboo (left). Eaten bamboo shoots from another forest (right).

Figure 2.3i Elephant eating grass (left). Broken Zingiberaceae herb (right).

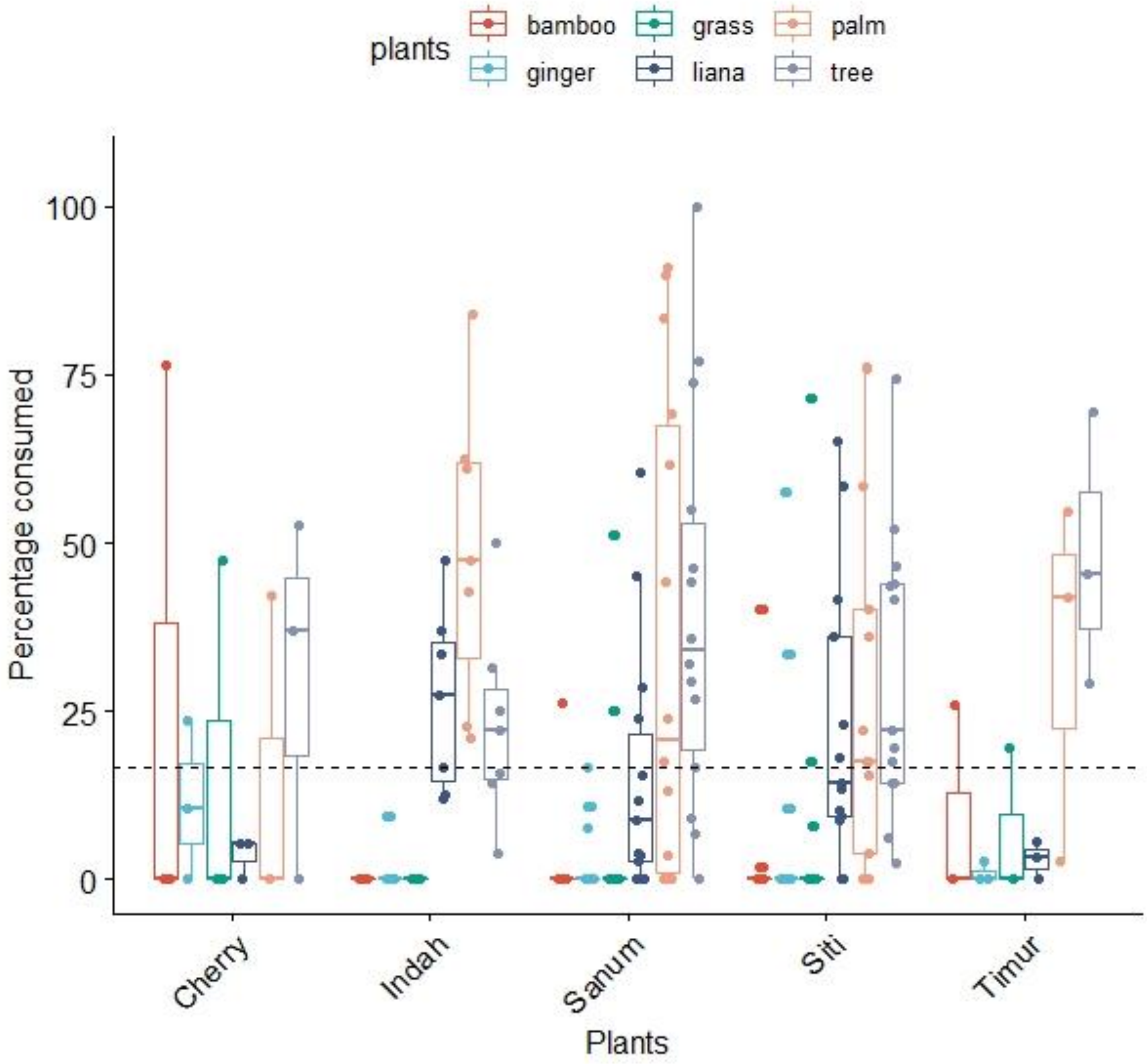


Figure A2.4 Percentage of plants consumed by different elephants (Cherry n= 3 observations, Indah n=7, Sanum n=14, Siti n=13, Timur n=3). Dotted line is observation mean of 16.7%.

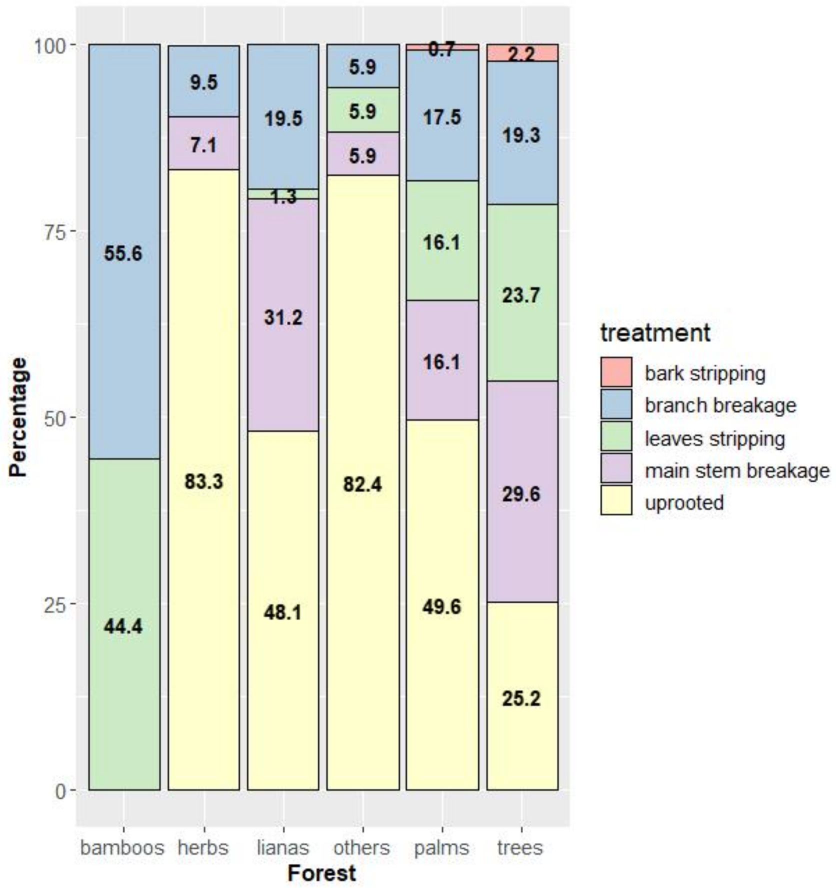


Figure A2.5 Herbivory impacts in closed forest from direct observations.

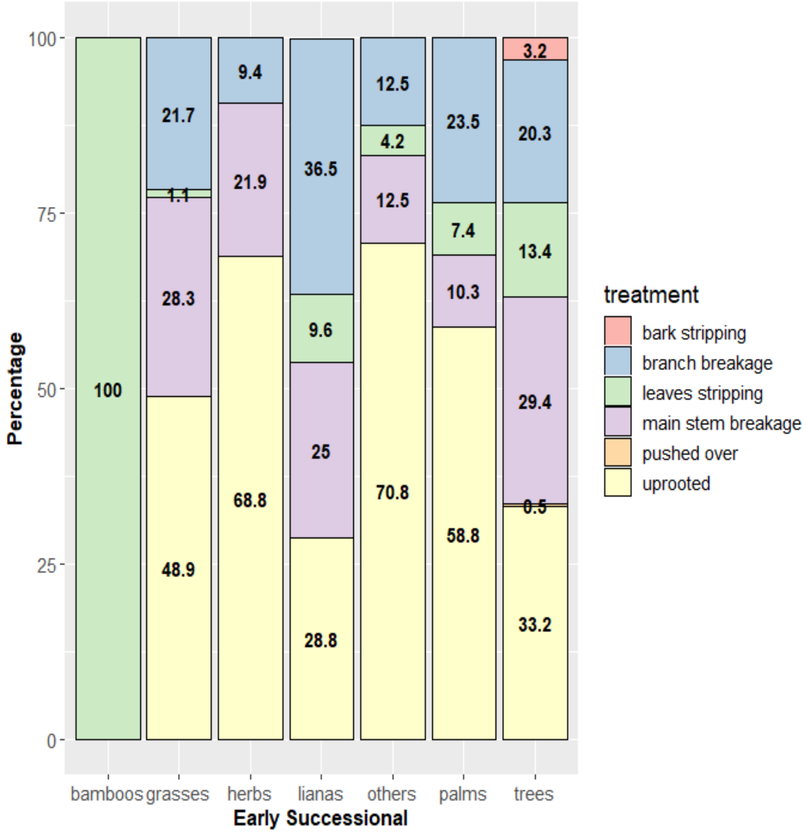


Figure A2.6 Herbivory impacts in early-successional habitats from direct observations

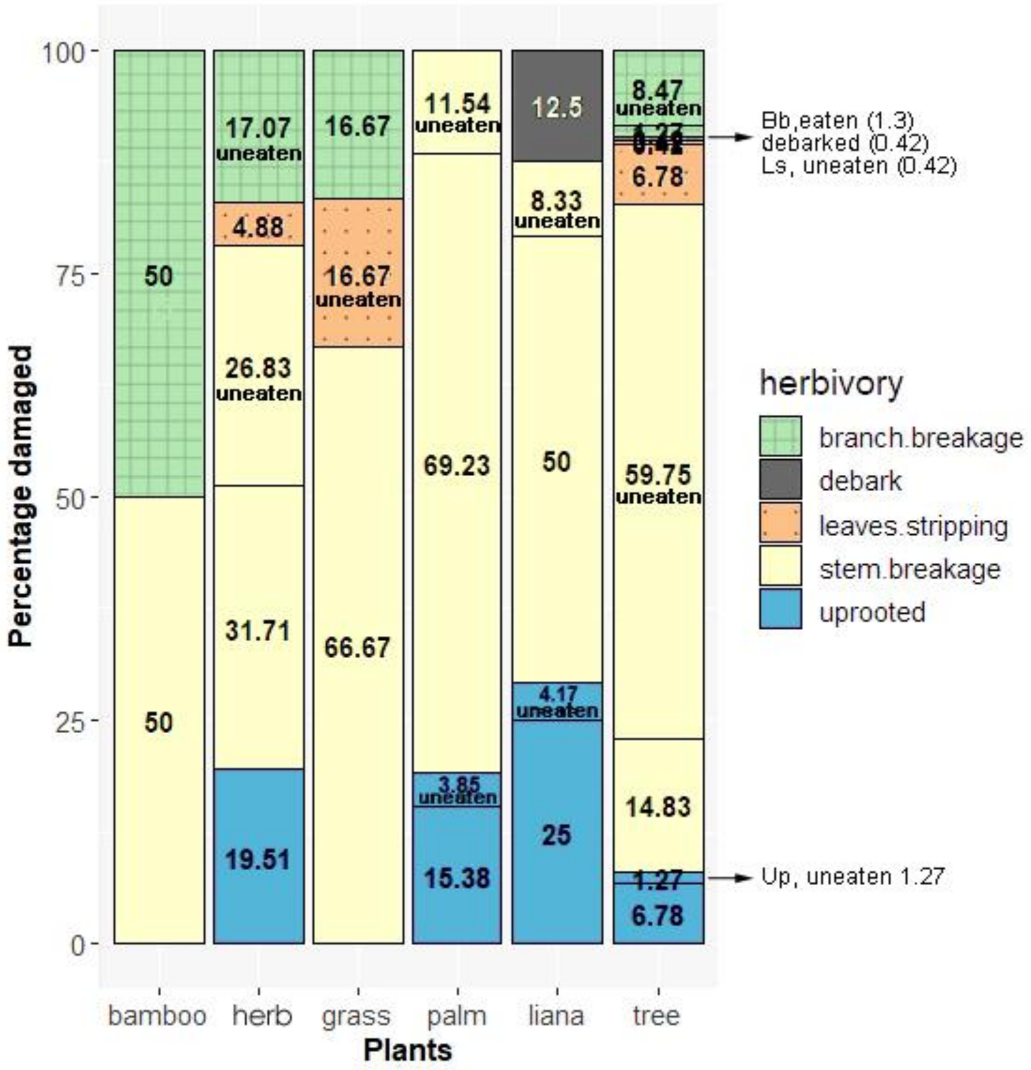


Figure A2.7 Proportional herbivory damage on plants above 1m tall, measured from foraged patches. Here, all broken grass is classified as stem breakage than uprooted. Most uprooted plants cannot be traced and uprooting was under-accounted with this method.

CHAPTER THREE

Elephant Frugivory and Wild Boar Seed Predation of *Irvingia malayana*, a Large-fruited Tree, in a Rainforest of Peninsular Malaysia

ABSTRACT

Irvingia malayana is a large-fruited and large-seeded tree species of Southeast Asia. As a large-fruited tree, it interacts with large mammal consumers, which either disperse or consume its seeds. In this preliminary study, I describe functional differences between Asian elephants (*Elephas maximus*) and wild boars (*Sus scrofa*) in their interactions with the fruits of *I. malayana* in a rainforest in northern Peninsular Malaysia. One camera trap was set up under each of five fruiting *I. malayana* trees for a total of 86 camera trap nights and a total of 145 independent visits from 12 vertebrate species was recorded. There were only two (1.4% of 145) visits by elephants, but they were the only animals to swallow *I. malayana* seeds (1.9% of 312 focal seeds). Wild boars were frequently recorded (29.7% of the animal visits), and they often acted as seed predators (consuming 24.4% of the 312 focal seeds). Besides these functional differences, an interesting temporal resource differentiation between the two species was also observed. Elephants consumed fresh fruits of one or two days old, while wild boars consumed fruits older than five days, probably when seeds could be accessed more efficiently. No animal species other than elephants were recorded to swallow the fruits of *I. malayana*, suggesting that elephants may be important dispersal vectors for this tree species in the tropical rainforest of Malaysia.

BACKGROUND

In tropical rainforests, vital ecological functions are maintained by plant-animal mutualisms such as pollination and seed dispersal (Dennis, 2007; Andresen et al., 2018). Seed dispersal is an essential process that allows seeds to reach potentially favourable sites to establish away from the parent plant (Herrera, 2002). The process of seed dispersal has long-term consequences on the spatial distribution, population structure, and survival of individual plant populations; as well as on organisms that are dependent on that plant species for their persistence (Nathan & Muller-Landau, 2000; Wang & Smith, 2002; Howe & Miriti, 2004; Markl et al., 2012). Plants have evolved morphological structures and various dispersal syndromes to overcome dispersal barriers (Herrera, 2002, Cousens et al., 2008). Seeds in humid tropical forests are especially adapted to animal dispersal, with 50 to 75% of tree species producing fleshy fruits (Howe & Smallwood, 1982).

While small fruits and large soft fruits with multiple small seeds have a larger assemblage of seed dispersers to depend on, large-fruited and large-seeded fleshy fruits are restricted to fewer dispersers, mostly large-bodied animals with a larger gape size (Corlett, 1998, Chen & Moles, 2015). Megafaunal syndrome fruits are fruits either of 4–10 cm in diameter with one to five large seeds, or fruits greater than 10 cm in diameter with multiple small seeds (Guimarães et al., 2008). In the Anthropocene, large-seeded plant species face a big challenge in sustaining their recruitment ability in increasingly fragmented and defaunated landscapes (Cramer et al., 2007; McConkey et al., 2012). The extinction of megafauna (often defined as animals more than 100 pounds or 44.5 kg; Martin, 1984) from South America around 10–15 Kyr BP has been linked to great losses in seed dispersal processes (Janzen & Martin, 1982; Guimarães et al., 2008; Doughty et al., 2016).

Little is known about the ecology of megafaunal-syndrome plants in tropical Asia. In Malaysia, there are large-fruited and large-seeded plant species (included but not restricted to megafaunal-syndrome plants) that may rely on large-bodied animals for their dispersal. Defaunation and megafauna loss in the region, however, is ongoing at a dramatic pace (Sodhi et al., 2004; Corlett, 2007) and the remaining large mammals might be inadequate to replace the largest seed dispersers. For example, Malayan tapirs (*Tapirus indicus*) disperse small-seeded plants but are seed predators for large-seeded ones (Campos-Arceiz et al., 2012), wild bovids disperse seeds over shorter distances and their digestive systems reduce seed germinability (Sekar et al., 2015), and gibbons are unable to swallow very large seeds (McConkey, 2000; McConkey et al., 2015). After the loss of two rhinoceros species (*Dicerorhinus sumatrensis* and *Rhinoceros sondaicus*; see Havmøller et al., 2015), Asian elephants (*Elephas maximus*) might be one of the few, sometimes the main, effective long-distance dispersers for large-seeded plants, providing high seed loads, long-distance dispersal, and reliable germination viability (Kitamura et al., 2007; Samansiri & Weerakoon, 2007; Campos-Arceiz et al., 2008; Campos-Arceiz & Blake, 2011). The impact of forest elephants on tropical tree diversity, however, remains unclear and has been questioned (see Hawthorne & Parren, 2000; and Blake et al., 2009, for contrasting opinions).

Seed predation is the consumption of seeds by animals (Janzen, 1971). Plants have evolved morphologically (e.g., strength, fibrous lignin, seed size variation, type), chemically (e.g., phenolic, terpenoid, alkaloid compounds, organic cyanides), and phenologically (e.g., synchronised mast fruiting) to defend themselves against such predation (Janzen, 1969; Silvertown, 1980; Waterman, 1984; Bodmer, 1991; Kelly & Sork, 2002). During mast fruiting, some plants escape the effects of seed predation through the strategy of predator satiation, producing large seed crop sizes to increase the chances for their seeds to escape (Janzen, 1971; Kelly & Sork, 2002; Xiao et al., 2013). Post-dispersal seed predation modulates the impact of seed dispersal and seedling colonisation on plant diversity, for example generating heterogeneity by means of scatter-hoarding (Janzen, 1971). This influence is driven at different spatial and temporal scales and establishment probabilities by animals of different guilds (Hulme, 1998, Jansen et al., 2004). In Southeast Asia, seed predation of fleshy fruits is mainly attributed to a few taxonomic groups such as tapirs, pigs, deer, squirrels, rats, and mice (Corlett, 1998; Campos-Arceiz et al., 2012). Little is known about their interaction with large-fruited plants.

In this study, I aim to differentiate the functional roles of the vertebrate consumers of *Irvingia malayana*, a large-fruited plant, in a tropical rainforest of Peninsular Malaysia. Specifically, my objectives are (1) to identify the potential seed dispersers and predators of *I. malayana* and (2) to quantify their impact in terms of the percentage of seeds they swallow or damage and the viability of ingested seeds.

METHODS

Study site – This study was conducted in Belum-Temengor Forest Complex (BTFC; 5°30'N, 101°20'E), in northern Peninsular Malaysia (Fig. 1). BTFC occupies an area of 3,546 km2 including the Royal Belum State Park (1,175 km2; gazetted in 2007), four permanent forest reserves (Temengor, Gerik, Banding, and Aman Jaya), and the man-made Temengor lake (Lim, 2010; Mohd Hasmadi et al., 2013; Hanis et al., 2014). BTFC is listed as an Environmentally Sensitive Area under Malaysia’s National Physical Plan and contains a crucial wildlife corridor under the Federal Government’s Central Forest Spine Masterplan to promote connectivity among major forest patches in Peninsular Malaysia (Government of Malaysia et al., 2014). The East- West Highway bisects the forest complex, dividing it into two large blocks (Fig. 3.1). Logging is permitted and ongoing inside the permanent forest reserves.

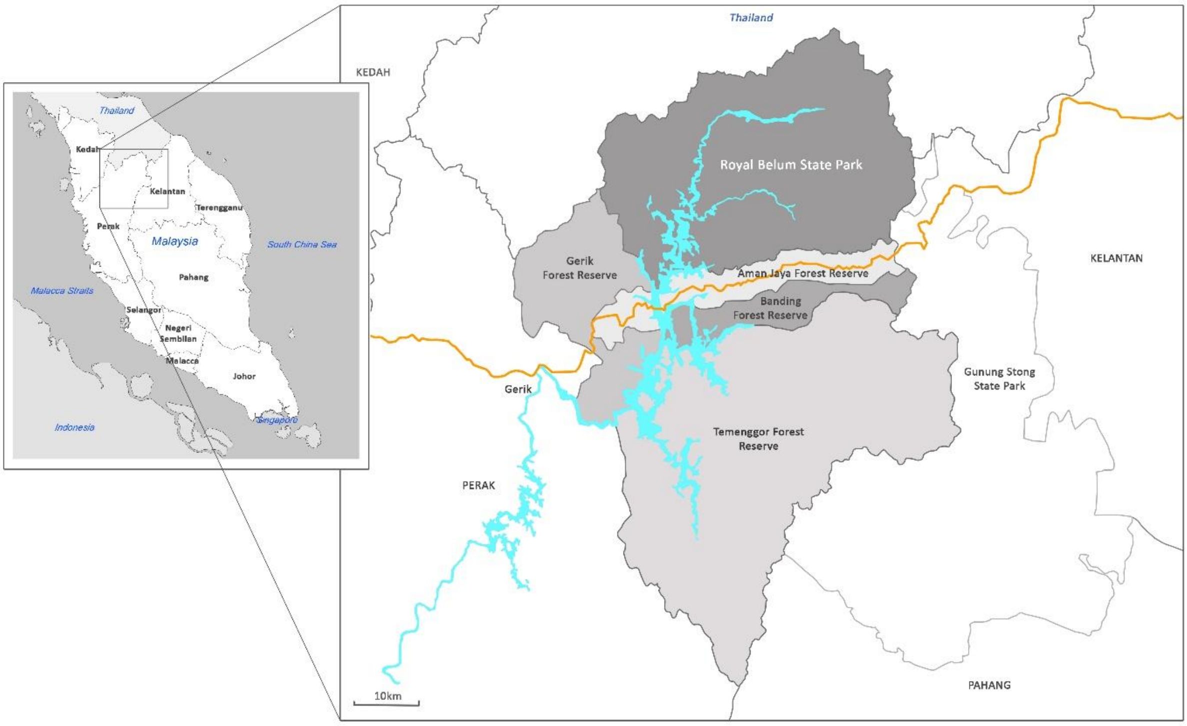


Figure 3.1 Map of Belum Temengor Forest Complex (BTFC), in Perak, northern Peninsular Malaysia.

In BTFC, elevation ranges from 130 m to 1,500 m above sea level, the mean daily temperature is 24.3°C (mean daily minimum 20.8°C, maximum 33.5°C), and humidity ranges from 70% to 98% (Mohd Hasmadi et al., 2013; Hanis et al., 2014). Meteorological records from Ayer Banun station (2012–2015) show an average precipitation of 2,140 mm annually, with the highest monthly rainfall from October to December (averaging 305 mm per month), and the lowest monthly in January and February (69 mm per month).

The dominant vegetation types in BTFC are lowland mixed dipterocarp, hill dipterocarp, and montane forests. Plant families with high tree diversity Euphorbiaceae, Dipterocarpaceae, Rubiaceae, Lauraceae, and Annonaceae (Chua et al., 2000). BTFC is also rich in wildlife including megafauna of conservation concern such as Asian elephants, tigers (*Panthera tigris*), leopards (*Panthera pardus*), gaurs (*Bos gaurus*), and Malayan tapirs (Or & Tang, 2011).

Focal plant species – *Irvingia malayana* is a large evergreen tree of spreading crown and massive buttress base growing up to 50 m tall and 50–129 cm in trunk diameter (Soepadmo & Wong, 1995; Van Sam et al., 2004; Ito et al., 2010). Recognised as a fruit tree of great significance for wildlife, (Svasti, 2000), *I. malayana* has large single-seeded ellipsoid fruits of 3.7–6.0 cm in length and 3.3–4 cm in diameter (Soepadmo & Wong, 1995; Kitamura et al., 2002; Van Sam et al., 2004). The fruits are fleshy, with thin green skin and yellow-orange fibrous pulp. A hard endocarp protects its seed with white cotyledons comprising 70% of saturated fatty acids and other oils (Bandelier et al., 2002). *I. malayana* is distributed throughout Indo-China, Thailand, and Malesia (Sumatra, Peninsula Malaysia, Borneo, and Bawean), and is found in various forest types including dry deciduous Dipterocarp forest, dry evergreen forest, tropical rain forest (Soepadmo & Wong, 1995; Van Sam et al., 2004). In Van Sam et al. (2004), its fruits are described as sweet and edible when ripe, and its seeds edible either cooked or raw. Extracts of *I. malayana* leaves inhibit neurotransmitter receptors of the central nervous system (Chung et al., 2005) and its wood contains 64eolignane, a phenylpropanoid commonly synthesised by plants to protect against herbivores (Mitsunaga et al. 1996).

The local name of *I. malayana* in Malaysia –'Pauh Kijang' – means 'fruit of the muntjac or barking deer' (*Muntiacus muntjac*; bin Kassim, 1987). Muntjacs are able to swallow the fruit and regurgitate the seed of *I. malayana* as described in Phillipps & Phillipps (2016). In Peninsular Malaysia, bin Kassim (1987) described *I. malayana* fruits as part of muntjacs diet, suggesting that they were able to swallow and disperse the seeds. *I. malayana* fruits have also been found to be consumed by long-tailed macaques (*Macaca fascicularis*) in Singapore (Lucas & Corlett, 1998); by sun bears (*Helarctos malayanus*; Fredriksson et al., 2006), leaf monkeys (*Presbytis rubicunda*), white-bearded gibbons (*Hylobates albibarbis*; Santosa et al., 2012), and orang utans (*Pongo pygmaeus*; Leighton, 1993; Hamilton & Galdikas 1994) in Borneo; and by Asian elephants in Thailand (Kitamura et al., 2007). Orang utans and squirrels have been described as seed predators of *I. malayana* (Leighton, 1993; Hamilton & Galdikas, 1994; Kitamura et al., 2002). In the studies by Kitamura et al. (2002, 2007), elephants were the only seed dispersers.

I. malayana has been observed fruiting during a mast fruiting period (Corlett, 1990). In BTFC, two fruiting episodes had been observed of this species between 2011 and 2016: one in October 2012 and another in July 2015. During both fruiting episodes, seeds of *I. malayana* were frequently found in elephant dung. In July 2015, my team and I scouted locations for signs of heavy fruit fall and collected 24 fruits to measure the sizes of both fruits and seeds.

Camera trapping – One camera trap (model Trophy Cam HD Bushnell; Bushnell.com) was deployed and baited with fallen and ripe *I. malayana* fruits under each of five fruiting *I. malayana* trees for up to 16 nights each in August and September 2015. Each camera trap was set twice (i.e., n= 5 camera trap × 2 bouts), after replacing the fruit bait, batteries, and memory cards. Two camera traps were deployed in Royal Belum State Park and three in Temengor Forest Reserve (Fig. 1). All camera traps were set near animal trails, placed approximately 0.5 m above ground. The camera traps were set up in video mode at 720 × 480 resolution, capturing 60 seconds per video, and a trigger delay interval of 1 second. The LED sensor level was set high, with a high night vision shutter. Date and time were stamped for analysis. To facilitate video analysis, the fruit baits were positioned in groups, and each group had no more than five fruits. The total number of fruits and fruit groups used as bait varied according to the number of fresh fruits available under each tree crown. A total of 286 bait fruits were used initially. During the camera trapping period, 30 fruits dropped from the tree within the camera's field of view, and ten additional fruits were added by the field crew on day 13; on the other hand, 14 fruits rolled outside the camera's field of view, making a final total of 312 bait fruits.

Germination test – To test the viability of *I. malayana* seeds after passing through an elephant gut, I conducted a pilot germination test using two seed (elephant-ingested vs. control seeds) and two substratum (elephant dung vs. forest soil) treatments. I planted a total of 109 *I. malayana* seeds: 40 seeds were retrieved from one elephant dung pile (hereafter ingested seeds) and 69 seeds were collected from fruits (and depulped by hand) beneath two *I. malayana* trees in the forest (hereafter control seeds). The different treatments were: (1) ingested seeds planted in dung (n=40), (2) control seeds planted in dung (n=31), and (3) control seeds planted in soil (n=38). I did not include the treatment 'ingested seeds planted in soil' because I was unable to find seeds in very fresh dung (i.e., immediately after defecation). All ingested seeds had spent at least a few hours inside elephant dung, therefore, compromising any attempt to test ingested seed germination in soil without the influence of dung. The germination test took place under shade in a roofed terrace. Seeds were deposited on the substratum and covered either by soil or dung soil thinly. Germination was considered as emergence of the radicle and monitored every two weeks. I discontinued the germination test after 14 weeks, when the germination curve declined towards a horizontal asymptote. The seeds that had not germinated after 14 weeks were cut open and examined to check if they were alive (still yellow and healthy) or dead (brown and infected).

Data processing and analysis – I recorded the number of independent animal visits and the animals' behaviour in relation to the *I. malayana* fruit baits. Animal species were identified following Francis (2008). Visits by the same animal species were considered to be independent if the camera traps were triggered at least 30 minutes apart at the same site. Animal behaviour was classified into six categories: no interaction (NI), interaction with no consumption (INC), flesh consumption (FC), whole fruit swallowing (FS), seed consumption (SC), and foraging off-plot (FOP) under the parent plant. No interaction refers to visits in which the animal(s)'s behaviour is not modified by the presence of the fruit (e.g., an animal passed by and ignored the fruits). Interaction with no consumption refers to visits in which the animal(s) did not consume fruit but their behaviour was affected by it (e.g., an animal passed by and sniffed the fruits but did not consume them). Flesh consumption refers to animal(s) observed eating the fruit flesh, but not the seeds (e.g., bit off small amounts of pulp). Whole fruit swallowing refers to fruit(s) being swallowed whole, not accompanied by any chewing or spitting. For seed consumption, seeds were observed to be chewed, usually accompanied by cracking sounds. Finally, foraging off-plots refers to events when the animals were captured foraging under the parent plant but away from the bait zone (hence making it difficult to assess their feeding behaviour). A visit may sometimes comprise two different interaction types. For example, a visit by wild boars may include both passing by and seed consumption by different individuals.

Germination measurements were processed following methods by Ranal & Santana (2006) and Ranal et al. (2009). Here, germinability is the percentage of seeds germinated by week 14. Mean germination time is the average number of weeks taken for the seeds to germinate. The coefficient of variation of germination is the percentage of variability concerning mean germination time. Uncertainty compares the spread of total number of seeds germinated – the higher the value, the higher the degree of uncertainty of germination. Synchrony measures simultaneous germinations – the lower the index, the higher germination is deemed synchronised.

RESULTS

Fruits of *I. malayana* (n=24) averaged 50.9 ± 2.3 mm in length, 42.1 ± 2.8 mm in diameter, and weighed 46.6 ± 5.2 g while the seeds averaged at 40.7 ± 2.5 mm in length, 28.5 ± 1.1 mm in diameter, and weighed 16.1 ± 1.5 g.

Two camera setups failed, which resulted in a final sampling effort of eight bouts (three cameras × two bouts, and two cameras × one bout) and a total of 86 camera trap nights. A total of 391 videos representing 145 independent visits by 12 vertebrate groups (11 mammal and one bird species; Table 3.1), excluding humans, were recorded. Three animal groups – rats, wild boars, and squirrels – accounted for 84.1% of all the visits (n=122). Three species – Asian golden cat (*Catopuma temminckii*), brush-tailed porcupine (*Atherurus macrourus*), and the crested partridge (*Rollulus rouloul*) were recorded just once. Of all the animal groups captured, only three – rats, wild boars, and elephants – consumed at least some part of the bait fruits; three groups – barking deer, squirrels, and bats – interacted with the fruits without consumption; while the others did not interact with the fruits (Table 3.1; Fig. 3.2).

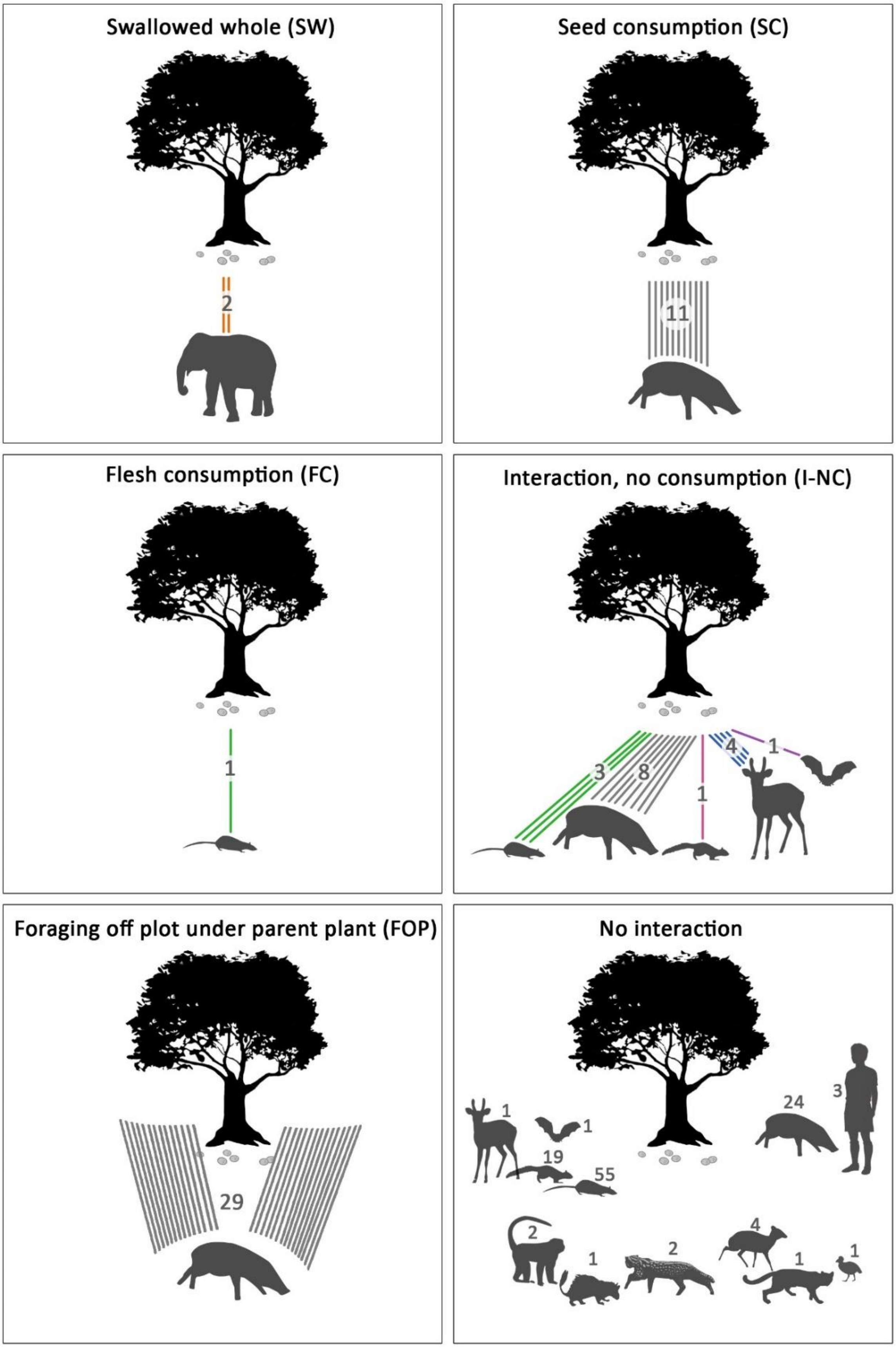


Figure 3.2 Type and frequency of interactions between vertebrates and *Irvingia malayana* trees, fruits, and seeds; each line represents one visit with the interaction type observed.

Table 3.1 Vertebrate visits and their interactions with *Irvingia malayana* fruits. NA = unidentified species; Visits = total number of independent visits; INC = interaction without consumption; FC = flesh consumption; SW = whole fruit swallowed; SC: seed consumption; FOP: foraging off-plot; NI = no interaction.

Animals (common name)	Family	Genus	Species	Visits	INC	FC	SW	SC	FO	NI
Rats	Muridae	*NA*	*NA*	59	3	1	0	0	0	55
Wild boar	Suidae	*Sus*	*scrofa*	43	8	0	0	11	29	24
Squirrel	Sciuridae	*NA*	*NA*	20	1	0	0	0	0	19
Barking deer	Cervidae	Muntiacus	muntjak	5	4	0	0	0	0	1
Greater mouse deer	Tragulidae	*Tragulus*	*napu*	4	0	0	0	0	0	4
Human	Homonidae	*Homo*	*Sapiens*	3	0	0	0	0	0	3
Asian elephant	Elephantidae	*Elephas*	*maximus*	2	0	0	2	0	0	0
Long-tailed macaque	Cercopithecidae	*Macaca*	*fascicularis*	2	0	0	0	0	0	2
Bats	Pteropodidae	*NA*	*NA*	2	1	0	0	0	0	1
Leopard cat	Felidae	*Prionailurus*	*bengalensis*	2	0	0	0	0	0	2
Asian golden cat	Felidae	*Catopuma*	*temminckii*	1	0	0	0	0	0	1
Crested partridge	Phasianidae	*Rollulus*	*rouloul*	1	0	0	0	0	0	1
Brush-tailed porcupine	Hystricidae	*Atherurus*	macrourus	1	0	0	0	0	0	1
Total				145	17	1	2	11	29	114

Rats were the most commonly captured animal on the camera traps, representing 40.7% (n=59) of the 145 independent visits. They consumed fruit flesh in one visit only (i.e., 1.7% of their visits) and interacted without consumption in three other visits (5.1%; Table 3.1). Wild boars were the second most frequently captured animals, in 29.7% (n=43) of the 145 independent visits. Wild boars predated on *I. malayana* seeds in 25.6% (n=11) of their visits, which they did by crushing the hard endocarp, with audible cracking sounds heard through the recordings (Fig. 3.3a, 3.3b). In 18.6% (n=8) of their visits, wild boars interacted with the fruits without consumption. In 67.4% (n=29) of their visits, they showed no interaction with the fruits but were observed foraging off-plot (i.e., under the same tree but far from the camera trap main field of vision). Wild boars visited four of the five focal trees. Elephants were recorded just twice (1.4% of all the 145 visits; at two different trees). In both visits, elephants swallowed fruits whole (Fig. 3.3c, 3.3d). Barking deer were recorded sniffing but did not consume any fruits in 80.0% of their visits (n=4); in the remaining 20% (n=1), barking deer had no interaction with the fruits. Of the two bat visits recorded, one captured a bat flying close to the fruits. Squirrels were frequently recorded, but they sniffed the bait fruits in only one case (Table 3.1).

Of the 312 bait fruits, analysis from the camera trap videos showed that 76 fruits (24.4% of the total) were consumed and chewed by wild boars and 6 fruits (1.9% of the total) were swallowed by elephants. The remaining fruits were left uneaten under the parent plant.

Figure 3.3 (a) Wild boars (*Sus scrofa*) consuming *Irvingia malayana* seeds; (b) crushed endocarps after being eaten by wild boars; (c) Asian elephants (*Elephas maximus*) consuming *I. malayana* fruits; (d) *I. malayana* seedling found in elephants' dung in the field.

Elephants and wild boars also differed in the timing of their fruit consumption. In both cases in which elephants were observed consuming bait fruits, the bait fruits were less than two days old – in one case, the fruits had been added (by the team) the day before; in the other, elephants consumed fruits that had naturally fallen from the tree about six hours before their visit. Elephants seemed to pick these fresh fruits while ignoring the old ones (Fig. 3.4a). Wild boars, on the other hand, seemed to prefer older fruits; whereby 78.7% of the fruits they consumed were eight days or older (Fig. 3.4a, 3.4b); average day of consumption by wild boar was 8.2 ± 2.1 days. In the first week since the bait fruits were set, wild boars consumed seeds in three out of 21 visits, sniffed and ignored bait fruits in seven visits, and were recorded foraging off-plot in 17 visits (Fig. 3.4b).

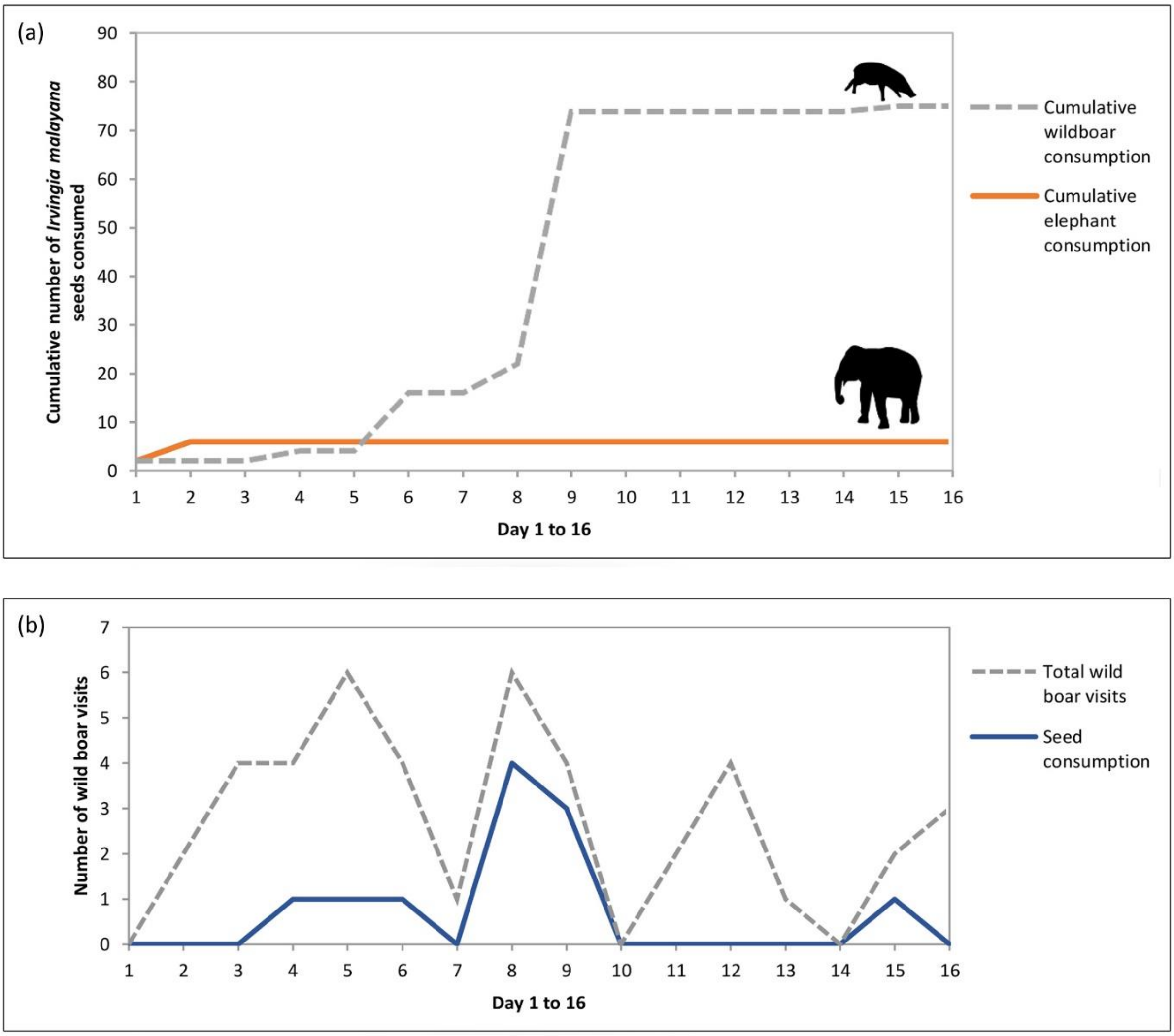


Figure 3.4 (a) Temporal differences in the consumption of *Irvingia malayana* fruits and seeds by wild boars (*Sus scrofa*) and Asian elephants (*Elephas maximus*). Note that elephants only consumed fresh fruits (< 2 days old) while wild boars consumed seeds from old fruits (generally > 5 days old); (b) Temporal distribution of all wild boar visits and their seed consumption.

Germinability was highest in control seeds planted in dung (96.7%), followed by control seeds in the soil (81.6%), and ingested seeds (75.0%; Table 3.2 and Fig. 3.5). Germination variability was high in all treatments (above 20%). Ingested seeds exhibited higher uncertainty (1.7) and lower synchronisation (0.6), compared to control seeds in dung (1.6 and 0.4, respectively) and in forest soil (1.0 and 0.6, respectively; Table 3.2). Ingested seeds exhibited a steeper germination curve compared to non-ingested seeds (Fig. 3.5). After 14 weeks, all the non-germinated seeds were found to be infected with fungus and dead.

Table 3.2 Results of germination test of *I. malayana* seeds using three different treatments. Treatments: D+IS = elephant-ingested seeds planted in dung; D+S = depulped control seeds planted in dung; S = depulped control seeds planted in forest soil. CV= coefficient of variation; germ. = germination.

Treatment	Germinability (%)	Mean germ. time (week)	CV germ. time (%)	Mean germ. rate (week^{-1})	Uncertainty	Synchrony
D+IS	75.0	3.9	34.0	0.3	1.0	0.6
D+S	96.7	5.0	35.8	0.2	1.6	0.4
S	81.6	6.3	20.8	0.2	1.7	0.3

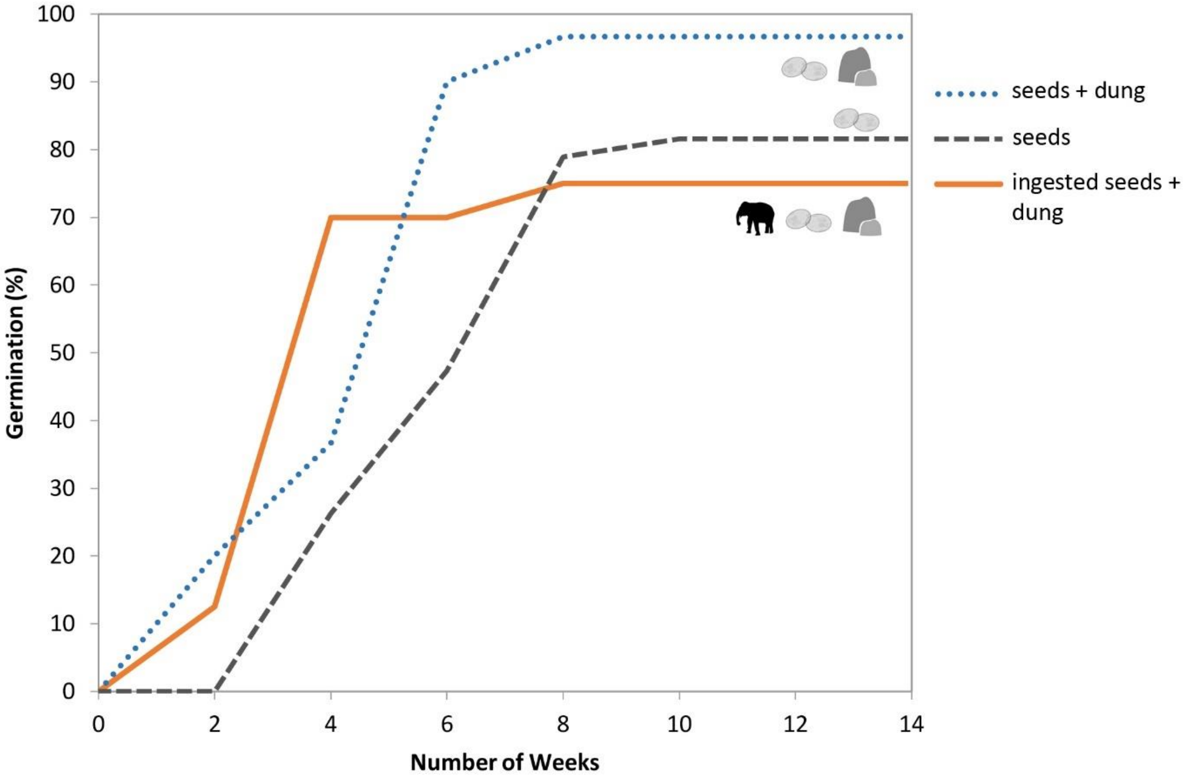


Figure 3.5 Germinability of *Irvingia malayana* seeds over 14 weeks. Treatments: D+IS = elephant-ingested seeds planted in dung; D+S = depulped control seeds planted in dung; S = depulped control seeds planted in forest soil.

DISCUSSION

In this study, I describe frugivory, seed dispersal, and seed predation interactions between a large-fruited and large-seeded tree species and the community of terrestrial vertebrates in a rainforest of northern Peninsular Malaysia.

Six mammal groups – wild boar, barking deer, rats, Asian elephant, bats, and squirrels – were found to interact with the fruits and seeds of *I. malayana*. Among these, only Asian elephants were observed to swallow the seeds, thus acting as seed dispersers, while wild boars were observed to be seed predators. Although elephants were the only seed disperser recorded in this study, they removed just 1.9% of the fruits. In Thailand, Kitamura et al. (2002) also found elephants to be *I. malayana*'s only seed dispersers, while squirrels were seed predators and wild boars were not included in their study.

The results of the small-scale germination test show that *I. malayana* seeds dispersed by elephants are generally viable (75.0%), although this percentage is lower than that of the manually depulped seeds. Having a hard endocarp in a fruit size easy for elephants to swallow, the seeds of *I. malayana* swallowed by elephants were unlikely to be damaged by chewing or digestion (Campos-Arceiz & Blake, 2011). Asian elephants provide effective long-distance dispersal while removing seeds from density competition, pathogens, and seed predation under parent plant (Augspurger, 1984; Campos-Arceiz & Blake, 2011; Sekar et al., 2015); they are thus likely to play a key role in the long-term survival and genetic diversity of large-fruited and large-seeded plants, such as *Irvingia malayana*.

While elephants were the only seed dispersers of *I. malayana* in this study, other terrestrial herbivores are known to consume the fruits and potentially disperse the seeds of this species. Barking deer were frequently recorded in the camera traps (17 visits) but they did not consume any of the fruit baits, although they have previously been described to swallow *I. malayana* fruits (bin Kassim, 1987; Phillipps & Phillipps, 2016). Larger terrestrial herbivores like sambar deer (*Rusa unicolor*), gaur, and Malayan tapir are likely to consume and disperse *I. malayana* but were not recorded in this study. Sumatran rhinos might have also contributed to the dispersal of *I. malayana* before they disappeared from BTFC at the beginning of the 21st century. Defaunation might, therefore, have reduced the number of effective dispersers of *I. malayana*, and the frequency of their visit in BTFC.

Primates also consume *I. malayana* fruits. In transects conducted by the authors in BTFC during the same period of this study, two (1.2%) out of 158 *I. malayana* fruits collected had been partially eaten by monkeys and the seeds dropped under the crown of the fruiting tree (K. McConkey, personal observation). BTFC primates include the long-tailed macaque, pig-tailed macaque (*Macaca nemestrina*), banded leaf-monkey (*Presbytis femoralis*), dusky leaf monkey (*Trachypithecus obscurus*), agile gibbon (*H. agilis*), and siamang (*Symphalangus syndactylus*). *I. malayana* seeds, however, are larger than what these primates can regularly swallow and disperse. Seeds swallowed by gibbons, for example, are smaller than 20 mm (McConkey, 2000); while the largest seeds swallowed by long-tailed macaques are approximately 3-4 mm (Corlett & Lucas, 1990). In Belum, primates are thus unlikely to be effective dispersers of *I. malayana* seeds to safe sites for successful germination (Schupp et al., 2010; McConkey et al., 2015).

Sun bears consume *I. malayana* fruits in Borneo (Fredriksson et al., 2006) but I did not record them in this study. Interestingly, I recorded an interaction between a bat and fruits of *I. malayana*, although I was unable to identify the type of bat in the video footage. The long-distance seed dispersal by large fruit bats can range up to 10 km. This, however, is limited to tiny seeds. For large seeds, fruit bats are able to disperse them from 100 m up to 1 km (Corlett, 2009).

In a previous study in a defaunated forest of Peninsular Malaysia, Yasuda et al. (2005) found the fruits of *I. malayana* to be neglected by many frugivores, despite a high abundance of fruits on the forest floor and a long observation period. It is likely that rodents such as porcupines and rats may provide some secondary seed dispersal to *I. malayana* seeds.

Wild boars acted as seed predators, destroying 24.4% (n=76) of the bait seeds, which they crushed despite *I. malayana* having hard endocarps. Wild boars seemed to have waited for the pulp of *I. malayana* fruits to turn soft before consuming them (Fig. 3.4). In Central Indonesian Borneo, Hamilton & Galdikas (1994) found orang utans to predate on *Irvingia malayana* – interestingly, *Irvingia malayana* seeds were a predominant part of orang utans diet in a period of three months (October to December 1980), while the orang utans had ignored them in previous fruiting years (Hamilton & Galdikas, 1994).

I observed what could be a temporal resource partitioning between a megafaunal syndrome plant's frugivore and a seed predator. Barnea et al. (1993) suggested that secondary compounds in pulp can deter bout consumption and encourage short visits to fruits to ensure dispersal being distributed over time. The plant might be favouring long-distance dispersal by megafauna prior to dispersal by less effective dispersers (Narconk et al., 1998; Sekar & Sukumar, 2013). While the benefits of elephants' dispersal are obvious, wild boars' seed crushing behaviour could also facilitate germination if seeds escaped when dropped (Narconk et al., 1998).

Should *I. malayana* be considered a megafaunal-syndrome species? In this study, the fruit sizes (50.9 × 42.1 mm) of *I. malayana* match the megafaunal fruit syndrome as defined by Guimarães et al. (2008) for the Neotropics (i.e., single-seeded fleshy fruit ≥ 4 cm in diameter). Additionally, the fruit and seed characteristics of *I. malayana* match other traits described by Janzen & Martin (1982) for megafaunal fruits: seeds protected by a hard endocarp that survive gut digestion, pulp rich in fats, and fruits that are dull green, indehiscent, which scatter over the ground slightly before ripening. In contrast, *I. malayana* fruits in other locations are smaller. In

Thailand, for example, fruits were 36.6 mm in length and 32.8 mm in diameter (Kitamura et al., 2002). It could be argued that *I. malayana* is at the fringe of the spectrum of a megafaunal-syndrome plant. It would be interesting to investigate geographical differences in *I. malayana*'s fruit and seed size and its relation with the local assemblage of dispersers.

Due to the small sample size, this study needs to be considered as preliminary. Only five *I. malayana* trees were studied for a short period. This is an inevitable limitation due to the difficulty to find more fruiting *I. malayana* individuals in the forest within the short fruiting period. Further studies with a larger sample size may reveal that other mammals (e.g., deer, wild cattle, tapirs, or sun bears) also contribute to the dispersal of the species. All the seeds used to test viability after being ingested by elephants were obtained from one single dung pile and therefore suffer from autocorrelation. The comparisons between germination treatments should be interpreted cautiously, but it is clear that *I. malayana* seeds dispersed by elephants retain high viability (75%, Fig. 3.5).

Despite these limitations, the results show that for the five *I. malayana* trees studied, (1) elephants removed a small number of seeds (2%) but were the only legitimate seed dispersers; (2) wild boars acted as seed predators, destroying nearly one quarter of the fruit crop; and (3) elephants and wild boars showed a temporal partition in their interactions with *I. malayana*, with elephants consuming only fresh fruits and wild boars mainly old ones. Defaunation (disappearance of rhinoceroses, the rarity of sambar deer and gaur) might be already having a negative effect on the seed dispersal of *I. malayana* and other large-fruited and large-seeded plants, even in relatively wildlife-rich forests such as BTFC.

CHAPTER FOUR

The Seed Dispersal Network of Royal Belum, a Megafauna-rich Tropical Rainforest

ABSTRACT

Large vertebrates occur at low densities and are mostly threatened by hunting and habitat degradation. Rare inclusion of large vertebrates in seed dispersal networks has hindered a robust understanding of the dynamics within seed dispersal communities, and the identification of functionally-unique species. I explored the seed dispersal system of a highly diverse and megafana-rich tropical rainforest in Malaysia. Through a combination of local ecological knowledge (LEK), field observations, measured fruit traits, and published records, I documented seed dispersal interactions from a broad range of seed treatments. The Belum seed dispersal network was nested (weighted NODF 26.3), modular (likelihood 0.289), and connected (weighted connectance, 0.14). I detected four modules. The first module included birds and 34 plant species, the second langurs, and 8 plant species. The third module comprised a mix of arboreal (e.g. Malayan flying fox, *Pteropus vampyrus*) and terrestrial mammals and 74 plant species, and the fourth included mainly seed predators, average-sized bats, and 30 plant species. Module three was the core module representing 50% of the seed dispersal interactions. In the network, gibbons (*Hylobates spp.*) emerged as the most effective and central seed dispersers. The Asian elephant *(Elephas maximus)* was a functional generalist important for the dispersal of central and large-seeded plant species, thus promoting variability in the community. In addition to gibbons and the Asian elephant, efficient seed dispersers such as binturong (*Arctictis binturong*), civets (Viverridae), and the Malayan sun bear (*Helarctos malayanus*) helped build network redundancy and resilience. Network modules were defined by hornbills and rats (as a large taxonomic group), gibbons, and Asian elephants. Wild boar (*Sus scrofa*), hornbills (family Burcerotidae), langurs (Cercopithecidae), and macaques were network connectors. Three *Ficus* spp. (Moraceae) and *Microcos cf. globulifera* (Tiliaceae) emerged as super-generalists. Important hub plants include *Aidia densiflora* (Rubiaceae), *Bouea macrophylla* (Anacardiaceae), three *Artocarpus* spp. (Moraceae), and *Garcinia parvifolia* (Ebenaceae). Many important seed dispersers are currently threatened and the network is not as robust as shown. Simulation of the loss of highly connected species showed a cascading effect on the plant community. As I utilised LEK to describe the network, I observed erosion of plant-animal LEK amongst the indigenous community. Urgent conservation efforts are required to conserve both highly functional but vulnerable species, and LEK pivotal to our understanding of the natural world.

BACKGROUND

Tropical Seed Dispersal Interactions, Peninsular Malaysia, Sundaic Region

Seed dispersal mutualistic interactions play a crucial role in maintaining biodiversity and the resilience of ecosystems (Terborgh et al., 2002; Thompson, 2009; Bascompte & Jordano, 2014 Andresen et al., 2018a). In neotropical forests, animals are important seed dispersers to more than 50–90% of canopy species and close to 100% of sub-canopy trees and shrub species. In Paleotropical forests, they disperse around 35–48% of canopy and 70–80% of sub-canopy species (Howe and Smallwood, 1982). The abundance and spatial distribution of dispersed fruit trees determine the population dynamics of frugivorous animals and, subsequently, predators further up the food chain (Wright et al., 1999). The seed dispersal process is pivotal to the maintenance of both the diversity and resilience characteristics of tropical forests (Jordano & Godoy, 2002).

The Indomalayan region harbours a great diversity of frugivores, including small invertebrates such as beetles and ants, at least two families of reptiles, 17 families of birds, and 12 families of mammals (Corlett, 1998). Sundaland resides within the Indomalayan realm, representing a large proportion of the tropical moist forests. In the Sundaic region, there has been ongoing progress with seed dispersal studies from a wide assemblage of animals (e.g. Lambert & Marshall, 1991; Kitamura et al., 2002; Hodgkison et al., 2003; Brodie et al., 2009; Nakashima & Sukor, 2009; McConkey & Brockelman, 2011; Marshall et al., 2014; Chanthorn et al., 2017). Many of these studies are species-specific and, while important, they provide limited insights in understanding the relative importance of different animals in the broader community. Seed dispersal studies that are conducted at the community-level are available from both Paleotropical and Afrotropical regions (Jordano et al., 2003; Sebastián-González et al.; 2015; Neuschulz et al., 2016; Dugger et al., 2018; Escribano-Avila et al., 2018), but few are available from the Paleotropics (Howe and Smallwood, 1982; Fleming et al., 1987). Research attention is needed for the Sundaic rainforests, both to account for the differences between biogeographic regions and to understand the trends governing the local interactions.

The role of large vertebrates in seed dispersal and forest regeneration is well recognized (E.g., Beck et al., 2013; Mueller et al., 2014; Naniwadekar et al., 2019). Several species serve as long-distance seed dispersers helping to connect isolated fragmented ecosystems (Couvreur et al., 2004; Campos-Arceiz & Blake, 2011; Mueller., 2014). Large terrestrial vertebrates could include megafauna (animals not less than 45.4 kg or 100 lbs; Martin, 1984), megaherbivore (animals with a body mass of at least 1000 kg; Owen-Smith, 1992), or the largest animal amongst a particular guild or taxa (e.g. hornbills amongst birds). They are absent from most studied seed-dispersal networks because the majority of network studies have been conducted in regions where the largest frugivores are already extinct. The importance of large frugivores and the implications of their loss to seed-dispersal networks require urgent attention as most species are threatened by human impacts (Vidal et al., 2013; Dirzo et al., 2014).

Amongst the largest frugivores, gaur (*Bos frontalis),* Asian elephants, and the critically endangered Javan rhinoceros (*Rhinoceros sondaicus*) are the only megaherbivores that still exist in Sundaland. The also extremely rare Sumatran rhinoceros (*Dicerorhinus sumatrensis*), has an average weight below 1000 kg (Sridhara et al., 2016), but was probably also once an important megaherbivore disperser. In Peninsular Malaysia, the last Sumatran rhino died in November 2019, joining the extinct Javan rhino and the Banteng (*Bos javanicus*) as megafauna lost from the Malaysian forests (Payne, 1990). Signs of gaur are rare in the forest. Elephants are the only megaherbivores that still retain good populations (estimated 1251–1466 in Peninsular Malaysia; Sukumar, 2006) and the only feasible option for us to study the functional role of megaherbivores in the forest. Asian elephants consume fruits of at least 122 species from 92 genera and 39 families (Campos-Arceiz and Blake, 2011), and are capable of dispersing large quantities of seeds over 1.2 km, with maximal distances of 4–6 km (Campos-Arceiz et al., 2008). In the rainforest, however, available seed dispersal studies of Asian elephants (e.g. Kitamura et al., 2002; Kitamura et al., 2007 in Thailand; Campos-Arceiz et al., 2008b in Myanmar; Varma et al., 2008 in Vietnam), showed lower levels of frugivory and higher variation in the number of seeds as compared to Asian elephants in the seasonal forest (e.g. Samansiri & Weerakoon, 2007 in Sri Lanka) and African elephants (Gautier-Hion et al., 1985; Blake et al., 2009; Babweteeraa et al., 2007). This study, thus, attempts to improve our understanding of the roles of megaherbivores as seed dispersers, focusing on the Asian elephants, and other medium and large-sized mammals — including the Pteropodid fruit bats, macaques, gibbons, ungulates, civets, and the Malayan sun bear in the seed dispersal network.

The loss of large mammals such as the Asian elephant, the Malayan flying fox, and hornbills will result in reduced fitness and genetic diversity in plant populations (Babweteera et al., 2007; Blake et al., 2009; Bunney et al., 2017). The loss of small vertebrates such as birds and bats can also lead to multitrophic cascades, subsequently affecting the abundance of herbivores and primary producers (Maas et al., 2015). We are living amidst a global wave of biodiversity loss. Defaunation of species is often non-random, and the consequences of species loss in ecological functioning and services are often latent (Hooper et al., 2005; Webb & Peart, 2008).

Some species carry unique ecological roles. The loss of pivotal species can compromise ecological functions held by these interactions, causing cascading consequences or state shifts in the community (Hooper et al., 2005). Preserving a functionally intact ecosystem has been of central concern for biodiversity maintenance (Mittermeier at al., 2003; Caro et al., 2011; Watson et al., 2018). Determining the consequences of defaunation at a community level is a pervasive challenge to ecologists.

The Sundaland is a biogeographic region that comprised a heterogenous continental core of Southeast Asia, including landmasses such as the Peninsular Malaysia, and the large islands of Borneo, Sumatra, and Java. It is divided by the Wallace line from the Sahul region of Sulawesi, Lombok (Eastern Indonesia), New Guinea, and Australia. In the Sundaic region, trees from the *Dipterocarpaceae* family dominate 50-80% of the rainforest canopy and emergent trees. Unlike many tropical forest species, dipterocarps mast-fruit intermittently in 3-10 years intervals. During the general fruiting period, several species produce massive fruit crops synchronously from the lowland to hill dipterocarp forests (Appanah, 1985; Sakai et al., 1999; Sakai, 2002). Dipterocarps are soil-specialists and some species are exceptionally adaptable to the nutrient-poor tropical soils (Baillie et al., 1987; Palmiotto et al., 2004). Towering above most other trees, they act as important carbon sinks of the forests (Pinard & Cropper, 2002; Saner at al., 2012; Kho et al., 2013). Dipterocarps, however, bear dry-winged nuts that are consumed mainly by rodents, wild pigs, and a few primates (Wells & Bagchi, 2005; Maycock, 2005; Chong et al., 2016). In the sub-canopy, Anacardiaceae, Burseraceae, Euphorbiaceae, and Myristicaceae are common families important to the frugivore community (Sakai et al., 1999). Trees from these families may fruit out of the general fruiting period, following fruiting frequencies such as sub-annual (fruiting in more than one cycle per year), annual (one major cycle per year), and supra-annual (one cycle more than a year) fruiting cycles. In an ecosystem with complex fruiting cycles and periodic high abundance of non-fleshy fruits, extremes in fruit availability may lead to negative consequences for frugivores and influence both frugivory and seed dispersal interactions. Food scarcity has been linked to animals such as bearded pigs (*Sus barbatus*) and the Malayan sun bear starving during inter-mast periods (Curran & Leighton, 2000; Wong et al., 2005; Fredriksson et al., 2006). The forest structure, fruiting phenomena, and low density of interactions, however, have made it highly challenging to conduct comprehensive observations of seed dispersal in this region.

In the Peninsular Malaysian rainforests, knowledge of plant-animal interactions is rooted in the minds of the forest-dwelling indigenous people, the 'Orang Asli'. The Orang Asli includes three major groups – the Negrito, Proto-Malay, and Senoi, and is represented by at least 18 sub-ethnic groups (Bolton, 1972; Or & Tang, 2011; Loke et al., 2020). Their livelihood may involve the collection of jungle roots, wild vegetables and fruits, slash-and-burn shifting cultivation, fishing, and hunting with traps and blowpipes (Bolton, 1972). At present, a minority continues to live as deep jungle nomads and settlers whereby hunting and gathering of forest food remains important (Lye, 2011). Most have resettled outside forest fringes, and they rely both on harvesting natural resources and small-scale farming of crops, rubber plantations, and the rearing of livestock to sustain their needs. They also harvest forest products such as rattans or resins (Or & Tang, 2011).

The Orang Asli has developed a strong relationship with the forest; the Batek, for example, regard themselves as 'people who dwell below tree cover' and are recognized for their 'arboricentric' intellect, using trees as land, property, kinship and time markers (Lye, 2005). To hunt and gather efficiently, the Orang Asli have grown to remember the physical terrain, accumulated knowledge related to forest, traditional medicine, wildlife, and the behaviour and habits of the animals well (Kuchikura, 1988; Kardooni et al., 2014). Fruits such as *Durio zibethinus, Baccaurea griffithii*, *Pakia speciosa,* and *Elasteriospermum tapos* are important sources of food for the Orang Asli (e.g. the Semang tribes) (Lye, 2005). Fruit gardens maintained by the Orang Asli (e.g. Chewong tribe) enhance both fruit tree abundance and mammal diversity in the forest (Moore et al., 2016). In the past, seeds of *Nephelium* sp. have been found intact in Proto-Malay faces (Cranbrook 1988 cited Ridley, 1893). The Orang Asli has developed a set of well-recognized traditional ethnobotanical and LEK, frequently tapped by ecologists to carry out their research efficiently. In recent years, ethnobotanical knowledge has received increased scientific prominence (Ellen, 1996; 1998). In the Neotropics, the importance of cultural heritage and indigenous knowledge was highlighted by Cámara-Leret et al. (2019). They found traditional knowledge is as vulnerable as species extinction, eroding quickly with cultural diffusion. In the Malaysian rainforest conducting field, observations are time-consuming and inefficient due to rugged and hilly terrains, elusive animals occurring at low densities, presence of dangerous animals such as elephants and tigers, and high faunal and floral diversity. Having a lack of established permanent scientific forest sites, LEK presents as a valuable resource that we could use to improve our understanding of plant-animal interactions in the Sundaic forest.

Network Concepts

Mutualisms, including seed dispersal interactions, are increasingly understood through a network perspective (Vázquez et al., 2009; Bascompte Jordano, 2007; 2014). The network approach helps shed light on the complexity of mechanisms underlying mutualistic interactions through graphs.

Several features characterize a network. Nodes and links form the basic building block of a graph (Euler, 1736; Erdös and Rényi, 1959). In ecological mutualistic networks, nodes represent species, and the 'degree' of a species is the number of links a node has. Nodes that tend to cluster together form a 'module'. Different modules may represent communities with distinct functionalities or hierarchies. Within the modules, plant or animal species may share similar traits, coming from similar functional groups (e.g., Donatti et al., 2011; Nogales et al., 2016). Nodes within a module are highly interrelated as compared to nodes from different modules.

In ecological networks, 'network modularity' defines the community structure of a network, quantifying the extent to which a network is organized in distinct clusters as compared to a null model. Nodes within a module are more strongly linked than nodes from other modules (Bascompte et al. 2007; Barber 2007). Networks with high modularity thus have dense connections within modules and sparse connections between nodes of different modules (Kashtan & Alon, 2005; Bascompte & Jordano, 2014). Comparing 51 pollination networks, Olesen et al. (2007) found that networks with more than 150 pollinator species were modular, but not networks with less than 50 species.

Studies on modularity facilitate our understanding of system structure, stability, and persistence in ecological networks (Thébault & Fontaine, 2010; Stouffer & Bascompte, 2011; Grilli et al., 2017). Modularity impedes extinction cascades (Rodriguez-Cabal et al., 2013; Nogales et al., 2016). High modularity has been related to flexibility in adapting to environmental changes, allowing for independent changes in different parts of the system, and avoiding strong changes to the overall system. In a highly fluctuating environment, such networks respond quickly to changes, promoting stability and persistence to the system (Teng & McCann, 2004; Stouffer & Bascompte, 2011; Valverde, 2017). Inferences that are drawn from modularity, however, are not always consistent (Webb & Bodin, 2008). The stabilizing effects of modular networks have been found to surface only under specific conditions (Grilli et al., 2016). Ecologically, while several authors relate biological networks to be shaped by evolution (Siegal et al., 2002; Proulx et al., 2005) or co-evolution (Nuismer et al., 2013), the modularity association with phylogenetic effects is unclear and may only be explained partially by shared evolutionary history (Donatti et al, 2011). Increasing modularity has also been attributed to environmental ecological factors such as climatic seasonality. Comparing 18 seed dispersal networks, Schleuning et al. (2014) found weak relationships between modularity and phylogenetic signals, such that modularity decreased consistently towards the tropics where seasonal turnover is less prominent.

Nestedness is another common characteristic of plant-animal mutualistic networks that infers organization and robustness to species extinctions (Bascompte et al., 2003; Fortuna et al., 2010; Pires et al., 2011). Nestedness prevents network disassembly (Memmott et al., 2004; Bascompte & Stouffer, 2009; Nogales et al., 2016). In a nested network, a few species control a high number of interactions. Generalised species with high degrees (e.g., generalist seed dispersers) tend to form a diverse assemblage. Specialised species with a low degree (e.g., specialist seed dispersers), would, in turn, interact with a smaller subset of the plant species that are linked to the generalist dispersers (Bascompte & Jordano, 2014; Mariani et al., 2019). Asymmetry in specialization is thus common in networks with a nested structure. The core of generalists may represent coevolutionary units, sharing roles akin to one another in ecosystem functionality. This presence of functional redundancy ensures system persistence following the extinction of some species (Bascompte & Jordano, 2014). High nestedness and modularity have been more prominent in pollination than seed dispersal networks. Much of what we understand from the latter, however, is contributed by dispersal studies related to birds (Dugger et al., 2017; Escribano-Avila et al., 2018).

In a community, not all species maintain vital roles in species interactions. Comparing 51 pollinator networks, Olesen et al. (2007) estimated that only 15% of all species were structurally important to the networks. These species were either 'hubs' or 'connectors. A network 'hub' is a node holding many more links than the average within that network. Between modules, few interactions are shared. Nodes sharing these interactions are 'connectors' that are not necessarily highly-linked but instead serve as bridges of connection between modules. The extinction of network connectors may cause modules to break apart. Ecologically, these species link different guilds within the community together.

To identify connectors and hubs of seed dispersal networks, Olesen et al. (2007) have implemented indices, known as c and z values, which define a species' importance in a network. c is calculated based on the distribution of interactions across modules (referred to as 'participation coefficient P' by Guimerà & Amaral (2005), while z is based on the distribution of interactions within modules. Species with low c (below 0.62) values and z (below 2.5) are peripheral species that interact with species within their module. Species with high c or z values are generalists either acting as connectors (high c and low z) or hubs (high z and low c value) in the network. Species exceeding the critical values (c=0.625; z=2.5) are super-generalists that act as both module hubs and connectors (Donatti et al., 2011; Olesen et al., 2007). Pollination networks are described with different thresholds (e.g., Memmott, 1999).

Apart from 'connectors' and 'hubs', indicators of centrality also help to describe the strength and central role of individual species and to evaluate their performance at different levels. Unlike hubs, a central node need not be highly connected. The 'closeness' of a node describes the centrality of a node by its path lengths to other nodes (Freeman, 1977). A species of high 'closeness' shares high adjacencies to a large number of species within the network. 'Betweenness' describes the centrality of a species by its position relevant to other nodes in the network and the number of shortest paths passing through it. A node of high 'betweenness' has a large influence over the service described in the network (Freeman, 1977; Estrada, 2009; Cagua et al., 2019). A species of high betweenness may help hold different parts of a network together and is capable of facilitating the spread of perturbations across the entire network (Coasta et al., 2019).

Theoretical ecology has benefited from the interpretations of network measures. A large proportion of network studies were based on birds (Mello et al., 2011; Dugger et al., 2017; Costa et al., 2018). Tropical studies that have explored community-based networks include the study of the spatial structure of seed dispersal across different habitats in Mozambique (Timóteo et al., 2018), invasive species in the Galápagos (Heleno et al., 2013), the restoration of the seed dispersal function in the Gorongosa National Park, Mozambique (Correia et al., 2016), the network of the hyper-diverse community of Brazilian Pantana (Donatti et al., 2011), and the seed-dispersal network of the Aldabra atoll (Wilfredo et al., unpubl.). In this study, I aim to produce a community-oriented seed dispersal network in the Sundaic region.

I aim to understand the structure of the seed dispersal network of the Royal Belum rainforest, representative of the Sundaic rainforest ecosystem. I will (1) describe the structure of the seed dispersal network at both network and community levels, (2) identify for functionally important seed dispersers, (3) evaluate the role of the Asian elephant, and (4) investigate the effects of defaunation on the network.

I achieve this by gathering data of frugivory and seed dispersal interactions through a combination of field observations, measured fruit traits, LEK, and published records. This network is the first seed dispersal network built through an inter-disciplinary approach, although the use of ethnobotany knowledge has been widespread for the fields of botany, forestry, agriculture, medicine, and utilization of wild plants (Hamilton et al., 2003). Being also the first community-oriented seed-dispersal network of the Sundaic region, this study is useful for comparisons to similar networks across other biogeographic realms. It enables us to observe the organizational patterns and functional differences that emerged from a network with extant megafauna. More specifically, it allows us to differentiate the importance of legitimate seed dispersal interactions by different animal groups and to identify key seed dispersers and plants that are important for maintaining the seed dispersal service. With the ongoing fast pace of defaunation, this study provides a baseline for understanding the robustness or fragility of defaunated systems that have reduced complexity.

METHODS

Study Area: Royal Belum State Park (RBSP), Belum-Temengor Complex, Malaysia

The Belum-Temengor Complex (5°30'N, 101°20'E) is a tropical rainforest in the Perak state of Northern Malaysia, that forms a transboundary complex with the Hala-Bala Wildlife Sanctuary and the Bang Lang National Park in Southern Thailand (Lim, 2010) (Fig. A4.01—A4.05). It encompasses an area of 3,546 km^2 that includes the RBSP (1,175 km^2; gazetted in 2007 as a strictly protected area), Temengor Forest Reserve (1,489 km^2; gazetted in 1991 as a Permanent Reserved Forest), three state land forests (Gerik, Banding, and the Aman Jaya forest), and a man-made Temengor lake (Lim, 2010; Rayan & Linkie, 2015).

The Belum-Temengor Complex is listed as an Environmentally Sensitive Area under Malaysia's National Physical Plan and contains a crucial wildlife corridor under the Federal Government's Central Forest Spine Masterplan to promote connectivity among major forest patches in Peninsular Malaysia (Government of Malaysia et al., 2014). However, the construction of the East-West Highway in 1975 divided the complex into two core forests, Belum to the North and Temengor in the South. The development of the 180km^2 Temengor Dam in 1977 for hydroelectric power had also led to the destruction of pristine lowland forests (Chye, 2010). From Sungai Perak, the dam extends 60km North and 30km South from the confluence of Sungai Perak, with an average depth of 40m and can hold 6,050 million m^3 of water (Davison et al., 1995). Damming has converted hilltops into islands of different shapes and sizes (Luki et al., 2014). While the RBSP is protected from commercial logging, the Temengor Forest Reserve is an active production forest where selective logging is permitted. The Temengor Forest Reserve is highly heterogenous, comprising of patches of logged, recovered, and small fragments of primary forests (Rayan & Linkie, 2015). The state land forests are also not protected from agriculture, plantations, or infrastructure developments by the state authorities.

BTFC ranges from 130 m to 2,160 m above sea level, with a mean daily temperature of 24.3°C (minimum 20.8°C, maximum 33.5°C), and humidity between 70 and 98% (Mohd Hasmadi et al., 2013; Hanis et al., 2014). The RBSP is comprised largely of hill dipterocarp (71.5%) mixed with lowland dipterocarp (5.6%), upper dipterocarp (20.9%) and montane forests (2.0%) (elevation 260m to 1533m). Common flora includes trees from Euphorbiaceae, Dipterocarpaceae, Rubiaceae, Lauraceae, and Annonaceae families (Chua et al., 2000). BTFC is rich in wildlife including flora and fauna of conservation concerns such as the Asian elephant, Malayan sun bear, Malayan tiger (*Panthera tigris*), the Indochinese leopard (*Panthera pardus*), gaur, and the Malayan tapir (*Tapir indicus*) (Or & Tang, 2011) (Fig. A4.03, A4.06). BTFC is also home to approximately 6310 Orang Asli mainly from the Jahai and Temiar ethnic groups. As a protected forest, RBSP has approximately 740 indigenous Orang Asli. Temengor houses the largest population of around 5000 people, and the Belum-Temengor State Land Forests has around 570 people (Rayan & Linkie, 2015).

All field data were collected over 16 months, along six transects located in the RBSP; these transects were a mean length of 1.1 ± 0.2 km (SD) and spanned a total distance of 6.7 km. Samplings were carried out monthly from August 2016 to November 2017. The transects in August and Sept 2016 varied in location but the sampled distance was approximately the same. From October 2016, I fixed the sampling locations along six transects: T1 (1.2 km), T2 (1 km), T4 (1.1 km), T5 (1 km), T6 (1 km), T3 (0.7km; August and September 2016) was relocated to T7 (1.4 km; October 2016) (Fig. 4.01). The total distance sampled for in August and September 2016 was 6km. The transects were positioned to run inland from the lake to avoid collecting data from areas subjected to higher edge effects (Reese & Ratti, 1988; Donovan et al., 1997). LEK was collected from villages located within both RBSP and Temengor Forest Reserve.

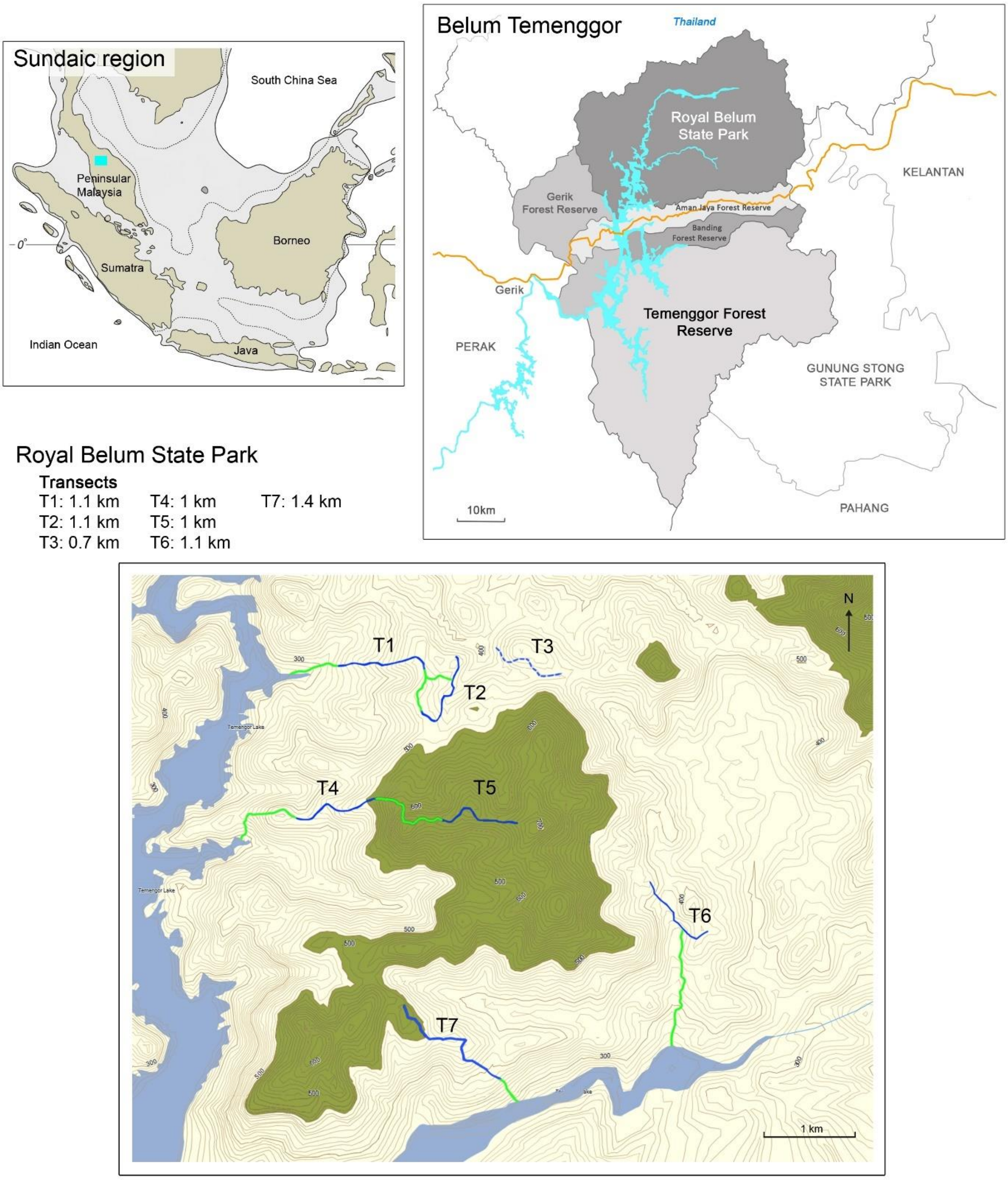


Figure 4.01 Map of Belum Temengor Forest Complex (BTFC), in Perak, northern Peninsular Malaysia, and location of transects within RBSP. Green lines are the main walking paths while blue colour lines are sampled transects (T1 to T7). I switched sampling from T3 (August, September 2016) to T7 from Oct 2016 to November 2017.

Interaction Matrix and Network Parameters

I gathered data on frugivory and seed dispersal interactions through a combination of (I) field observations, (II) measured fruit traits, (III) LEK, and (IV) published records. In the Belum-Temengor forest, poaching activities are prevalent, and animals are highly adapted to both predators and hunting (Oi & Tiang, 2011; Loke et al., 2020). Hence, conventional tree watches and camera-trapping techniques were impractical to capture the seed dispersal interactions of this highly diverse network within the short study period of around 2 years. The use of information from all four approaches ensured a comprehensive description of the network.

Seed Dispersal Interactions – Fruit-eating animals handle seeds in diverse ways, and many frugivory interactions do not result in successful seed dispersal. Because seed handling by animals is difficult to observe and the fate of seeds are difficult to track, frugivory interactions can be wrongly assumed as dispersal. Furthermore, other forms of effective dispersal that do not involve swallowing and defecating seeds can also be neglected (sensu Corlett, 1998; Feer et al., 2001). Seeds that I wished to exclude were fragmented and predated (not hoarded) seeds. Alternative forms of dispersal that I wished to include in this study were different ways in which seeds were carried away from the parent tree. For example, hoarding, seed spitting, and regurgitation (Table 4.01):

Table 4.01 Dispersed and undispersed seed treatments

Dispersed seeds	Undispersed seeds
seeds swallowed and defecated	seeds defecated and fragmented
seeds carried and spat	seeds predated and not hoarded
seeds regurgitated	
seeds predated and hoarded	

(I) Field Observations

Transects – My team and I monitored the fruiting phenology of the RBSP along transects to (i) document the fruit species in the system and their availability, (ii) to gather local plant names and photographs to be used in the interviews (LEK), and (iii) to obtain fruit samples to measure and describe fruit traits. We also (iv) obtained additional data on fruit and seed handling interactions from animal feeding signs on fruits and seeds, and camera traps set up under fruiting trees.

We carried out monthly sampling over 16 months, from August 2016 to November 2017 (Fig. 4.01). In July 2016, we cleared the trails of old fruits. In the selection of transects, we avoided terrains with steep slopes according to the topology shown in the global positioning system (GPS) unit. Transects were spread out as far as possible, such that we could complete sampling within three days, with either two or three field teams. Except for T1 and T2 (due to terrain difficulties), all transects were at least 700 m and up to 5 km away from one another.

The fruiting phenology of RBSP was monitored by a combination of methods. Only plants from adult trees that were larger than 10cm diameter at breast height (dbh at 1.3m) or lianas with a stem size larger than 2cm diameter were included, as suggested by Burnham 2002 and Kurzel et al., 2006 for examining the diversity of canopy lianas. Fruits of both zoochoric or non-zoochoric plants were collected as even the latter are food to many seed predators such as langurs (Adhikaree & Shrestha, 2011) and macaques (Lucas & Corlett, 1998). All fruits were included in the interviews and the networks.

We scanned the ground for fallen fruits over 1.5m width along six transects (total 6.7 km; mean 1.1 ± 0.2 km) (Corlett, 1990; Feer & Forget, 2002). Upon spotting a fruit, we measured ground phenology and feeding signs using one 1m^2 quadrat along the transect, and two 1m^2 quadrats under the tree canopy (sensu Wieczkowski, 2013). We searched for the fruiting plant location up to a perpendicular distance of 15m away from the main transect, marked (with GPS), and tagged the plant with an individual ID. We checked all marked tree for at least three months for fruiting and feeding signs, keeping track of fruiting phenology both on the plant tags (A6 size) and the datasheets. We used GPS with navigation distance error of up to 15m (Garmin 2020), or depended on the memory of the Orang Asli assistants to return to marked trees. During the process, several tags were damaged or removed by poachers, further complicating the attempts to relocate trees. As not all trees were easy to be relocated, we stopped returning to a tree when it did not fruit for two months. For example, when fruits were found in May but no fruits were detected in June and July. However, we continue to search for fruits along the transects, and if fruits of a marked tree were found again, we repeated the cycle of tree checking.

Over the sampling period, our Temiar Orang Asli field assistants quickly became familiarised with the trails, remembering the locations of several trees and camera set-ups. Their skills enabled us to accomplish the sampling efficiently, on top of the use of GPS. The trail method is an economical and practical method for assessing community phenological patterns. Combined with quadrats and at least two months of consistent checking on non-fruiting trees, we were able to collect a substantial amount of information to describe the fruiting trends and provide a robust collection of species and their feeding interactions. This method enabled us to efficiently cover a large spatial scale at which these animals forage. Video footages from camera traps revealed that the trails are often utilised by focal terrestrial fauna such as the sambar deer (*Rusa unicolor*), the Malayan sun bear, gaur, and the Asia elephant.

We did not manage to locate and identify the local names of 25 fruiting plants (of a total sample of 175 species), 11 of which were small-fruited unidentifiable singletons or doubles and were mostly lianas. These trees were excluded from the analysis due to the difficulty in identifying the species and quantifying their interactions. The other 14 unlocated trees were included in the sample as they were either previously collected species (between July 2015 and July 2016) or identifiable large-fruited species with a local name.

Interaction quadrats – We recorded interactions from feeding signs in 1m x 1m quadrats (termed an interaction quadrat) (Appendix Fig. A4.07—A4.11). For larger fruits (above 4cm diameter) that could not be adequately sampled in the 1m x 1m quadrats, we used bigger quadrats (1m x 2–4m). At least one quadrat was positioned on the transect and two under the crown of the parent plant. For species with more than two individual fruiting plants within the same month, fewer quadrats were sampled under the parent plants if time was limited. We recorded the animals that were responsible for the feeding signs left on fruits and seeds, based on our Orang Asli field assistants' judgments of the teeth marks. Teeth marks identified were assigned as monkeys (sometimes langurs or macaques could be specified), gibbons, squirrels, porcupines, rats, bats, and deer.

LEK of local indigenous assistants is accumulated from long-term observations, i.e., since they were exposed to the forest as a child. While ecologists may collect evidence from a sampling period, the indigenous people are exposed to low and peak fruiting seasons throughout the year. They may identify a foodplant by how frequently an animal was spotted feeding at the tree. In addition to teeth marks, they may differentiate species by the differences in feeding frequencies or feeding signs found under a tree. For example, squirrels may feed consistently and drop seeds with tiny fragments under a tree, while macaques may visit a tree, clean fruit pulp off a seed, before dropping it under a tree. Other evidence may include footprints, claw marks, known territories, the way animals scatter seeds (e.g. regurgitation by deer could be found as single spat seed along trails, with additional piles of regurgitated seeds under fruiting trees), animal behaviour, presence of scats or dung, size of fruits and seeds, fruit traits, etc.

Camera traps – During the survey, most fruiting trees had few fruits underneath them that could be used as baits for camera trap set-ups. Some fruits were too small or old to be used as fruit baits. We set up camera traps beneath the fruiting trees for species with at least two to four large fresh fruits (fruit diameter ~4cm), or eight to ten medium-sized fresh fruits (fruit diameter 1.5–4 cm) available (Appendix Fig. A4.12—A4.14). We also gathered a mixture of fruit species (species with too few fruits or abundant fruits) to camera trap them in a mineral lick (Sira Gajah in Temengor) highly utilised by wildlife to increase the chance of recording any possible interactions. We arranged fruit baits within a grid to allow us to determine fruit removal more easily. Throughout the sampling period, 61 camera traps of 35 plant species were successfully retrieved back with recorded video footage. More than 15 camera traps were stolen by poachers, and a few were damaged by elephants. It was impractical to secure the camera traps permanently as this study required frequent relocations according to new fruiting plants. We avoided setting up co-ordinates for the video set-ups to prevent poachers from abusing the stolen information.

***Seeds in scats or dung* –** We collected seeds in scats or dung along the transects when available (Fig. A4.15—A4.16). However, we found this method ineffective in this landscape (as supported by Olivier, 1978), as most faecal materials were hard to find, quickly washed out by rain or removed by insects such as dung beetles. Elephant dungs were the most obvious, although we also encountered defecations of civets, bovid, the Malayan tapir, and wild boar. Even so, only three plant species were recovered from the elephant dung.

(II) Measured Fruit Traits

164 plant morphospecies were collected from the seven transects. A total of 613 individual plants, including 526 trees, 83 lianas, and 4 palms were sampled. They represent fruits from at least 43 families and 93 genera, of which, 22 species were unidentifiable. A complete list of plants can be found in Appendix Table A4.1. As often as possible, leaves and photographs of different plant features (trunk, crown, leaves, intact fruits and seeds, cross-sections of fruits and seeds) were collected. All fruit and seed measurements, as well as other fruit traits, were recorded. Measurements used for this study include fruit and seed weight and diameter, and seed number. Fruit traits include fruit type (indehiscent dry, indehiscent fleshy, dehiscent dry and dehiscent fleshy fruit), skin piercing (easy, moderate, difficult), and seed hardness (soft, soft-medium, medium, medium-hard, hard).

When the fruit crop was large, I measured at least 30 samples for each species. This process required a consistent comparison of fruit sizes throughout different months, such that only mature fruit sizes were used for analyses. It was not possible to judge all mature fruits by their colours as many fruits either remained green or were not detected a second time. Many sampled plants, however, fruited in low quantity and had partially damaged fruits with seeds missing. In comparison to the study of a specific focal plant species, measuring large numbers of fruits and seeds may be impractical for a community-oriented study. For future studies with resource constraints, I recommend measuring around 10 intact mature fruits from each tree per sampling, thereafter, accumulating more measurements overtime.

Plant identification – The local indigenous names provided by different field assistants can be different, and not all plants were familiar to our Orang Asli assistants. Photographs of leaves, fruits, and seeds were taken at different angles (from 526 trees), as well as pressed leaves (herbarium) allowed for further corrections of names. This is a tedious but important process to help improve the quality of the dataset. Being familiar with all fruit species would help facilitate this error correction process. The full fruit trait records for each species is also more detailed than what was used for analysis (e.g., dehiscent dry capsule to describe the fruit type; colours of fruits and seeds, skin thickness, odour, etc.).

For species identification, I gathered a list of the common plants of BTFC from available resources. From this list, I web searched to consolidate a pictorial library that includes fruits, seeds, leaves, and herbarium of these plants. I prioritised pictures from botanical institutions or herbariums. However, I found herbariums not always helpful for fruit comparisons as compared to more informal sources (e.g. photo galleries of botanists or photographers). I matched the collection of fruits, seeds, and leaves pictures with this pictorial library. When plants were unidentifiable with the Belum plant library, I expanded possible matching to a Perak plant list (compilled by Dr. Lim Teck Wyn from Turner, 1995). This method allowed us to match most plants to the genus level. I indicated unidentified plants with an asterisk attached to the Temiar name (e.g., Cabol Kedik*).

(III) Interviews with indigenous people and the Utilisation of LEK

As mentioned earlier (Field Observations: Interaction quadrats), forest-dwelling indigenous people can possess detailed knowledge of plant-animal interactions that have been accumulated through personal observations required for hunting purposes and as life skills. They also acquired knowledge from their elders and share skills among themselves. I interviewed Orang Asli belonging to the Jahai (sub-ethnic of Negrito) and Temiar groups (sub-ethnic of Senoi) — the major groups of Orang Asli living in BTFC. In the present day, some Orang Asli retain skills of fishing, hunting, and gathering from the forests, and some hold main-stream jobs (e.g. working in factories, tourism, etc.). Many Jahai people in BTFC still live in proximity to the forests, fishing, hunting, and gathering for food. Most Temiar people are settled in Temengor with concrete housings and plantations surrounded by forests recovered from logging activities. They occasionally hunt, gather, and collect products such as honey from the forest.

To utilise the LEK, I designed an interview to help identify different seed treatments of forest plants by a wide selection of animal taxa (Lee, 2002; Avibase— Lepage, 2003; Francis, 2008). From the guidebooks, I identified 47 animal taxa common to the community but reduced this to 34 taxa for the final network. Some taxa were eliminated due to poor quality of information or the taxa rarely disperse seeds (e.g. dhole). Animals represented in the Belum seed dispersal network are listed in Table 4.02. Some large-bodied species such as the Asian fairy-bluebird (*Trena puella*) were presented individually, rather than within a species group. Taxa comprising of multiple species are named in their plural form (e.g. barbets), and single-species are listed using their common names (Asian fairy-bluebird). This naming convention is applicable throughout the chapter to facilitate results interpretation.

Malaysia, including Sabah, Sarawak and Peninsular Malaysia, has a total of 718 species of birds, of which 580 are land birds, 32 are seabirds, 239 are migratory birds and 124 are water birds. 62 bird species are globally threatened. Endangered land bird species that can be found in Peninsular Malaysia include the green peafowl (*Pavo muticus*), crested argus (*Rheinardia ocellata*), white-rumped vulture (*Gyps bengalensis*), slender-billed vulture (*Gyps tenuirostris*), white-crowned hornbill (*Berenicornis comatus*), wrinkled hornbill (*Aceros corrugates*). Critically endangered species include helmeted hornbill (*Rhinoplax vigil*) and straw-headed bulbul (*Pycnonotus zeylanicus*). Birds are under-represented in the seed dispersal network, but their inclusion provides a comparison to the roles of mammals in terms of the identity of fruit species dispersed and also how they uphold the organization of the network.

Table 4.02 Animals in the seed dispersal network of Belum, and examples of species present and their respective IUCN status (IUCN red list, last assessed year). Only species with concerned status are listed for birds of a diverse group.

Animal **Birds**	**Order**	**Family**	**Examples of Genus / Species (IUCN)**
Asian fairy-bluebird	Passeriformes	Irenidae	**Least concerned (2016):** *Irena puella*
Barbets	Piciformes	Megalaimidae	**Near Threatened (2016):** Red-crowned barbet (*Megalaima rafflesii*), Red-throated barbet (*Megalaima mystacophanos*), Yellow-crowned barbet (*Megalaima henricii*) (Lim, 2010) **Least concerned (last assessed):** Gold-whiskered barbet *(Psilopogon chrysopogon,* 2018*),* Blue-earned barbet (*Psilopogon australis,* 2016), Brown barbet (*Caloramphus fuliginosus,* 2016)

(continued) Table 4.02 Animals in the seed dispersal network of Belum

Animal	Order	Family	Genus / Species (IUCN)
Doves	Columbiformes	Columbiformes	**Least Concern (last assessed):** Spotted-necked dove (*Spilopelia chinensis*, 2016), Grey-capped Emerald dove (*Chalcophaps indica*, 2016).
Bulbuls (20 or 26 Malaysian species)	Passeriformes	Pycnonotidae	**Critically Endangered (2018):** Straw-headed bulbul (*Pycnonotus zeylanicus*) **Near Threatened (2016):** Scaly-breasted bulbul (*Pycnonotus squamatus*), Grey-bellied bulbul (*Pycnonotus cyaniventris*), Puff-backed bulbul (*Pycnonotus eutilotis*), Finsch's bulbul (*Alophoixus finschii*), Buff-vented bulbul (*Iole olivacea*), Streaked bulbul (*Ixos malaccensis*) (Lim, 2010)
Great Argus	Galliformes	Phasianidae	**Near threatened (2016):** *Argusianus argus*
Green pigeons	Galliformes	Columbidae	*Treron spp.*: **Least Concern (last assessed):** Little green pigeon (*Treron olax,* 2018), Thick-billed green pigeon (*Treron curvirostra,* 2018), Large green pigeon (*Treron capellei, 2016*)
Hill Mynah	Passeriformes	Sturnidae	**Least Concern (2016):** Hill Mynah (*Gracula religiosa*)
Hornbills	Bucerotiformes	Bucerotidae	**Critically Endangered (2018):** Helmeted hornbill (*Rhinoplax vigil*) **Endangered (2018):** White-crowned hornbill (*Berenicornis comatus*), Wrinkled hornbill (*Rhabdotorrhinus corrugatus*) **Vulnerable (2018):** Great hornbill (*Buceros bicornis*) Rhinoceros hornbill (*Buceros rhinoceros*), Wreathed hornbill (*Rhyticeros undulates*), Black hornbill (*Antharacoceros malayanus*) Plain-pouched hornbill (*Aceros subruficollis, 2016*) **Near threatened (2018):** Bushy-crested hornbill (*Anorrhinus galeritus*), **Least Concern (2016):** Oriental pied hornbill (*Anthracoceros albirostris*)

(continued) Table 4.02 Animals in the seed dispersal network of Belum

Animal	**Order**	**Family**	**Genus / Species (IUCN)**
Ioras	Passeriformes	Aegithinidae	**Near Threatened (2016):** Green iora (*Aegithina viridissima*), Great iora (*Aegithina lafresnayei)* (Lim, 2010)
Jays	Passeriformes	Corvidae	**Near Threatened (2019):** Crested Jay (*Platylophus galericulatus*)
Leafbirds	Passeriformes	Chloropseidae	**Endangered (2019):** Greater green leafbird *(Chloropsis sonnerati)* **Near Threatened (2016):** Lesser green leafbird (*Chloropsis cyanopogon*) **Least Concern (2016):** Blue-winged leafbird (*Chloropsis moluccensis*)
Nuthatches	Passeriformes	Sittidae	**Least Concern (2016):** Velvet-fronted nuthatch (*Sitta frontalis*)
Parrots	Psittaciformes	Psittaculidae	**Near Threatened (2016):** Blue-rumped parrot *(Psittinus cyanurus),* Blue-crowned hanging parrot (*Loriculus galgulus*)
<u>**Arboreal mammals (except rodents)**</u>			
Bats	Chiroptera	Pteropodidae	**Least concerned (last assessed):** Lesser dog-faced fruit bat (*Cynopterus brachyotis, 2019*), Spotted-winged fruit bat *(Balionycteris maculate, 2008*), Lucas's Short-nosed fruit bat (*Penthetor lucasi, 2008*) Black-capped fruit bat (*Chironax melanocephalus, 2008),* Geoffroy's rousette (*Rousettus amplexicaudatus, 2019*)
Malayan flying fox	Chiroptera	Pteropodidae	**Near threatened (2008):** *Pteropus vampyrus*
Gibbons	Primates	Hylobatidae	**Endangered (2008):** Lar Gibbon (*Hylobates lar*), Agile gibbon (*Hylobates agilis*)
Langurs	Primates	Cercopithecidae	**Near threatened (2008):** White-thighed Surili (*Presbytis siamensis*), Dusky leaf monkey (*Trachypithecus Obscurus*), Banded leaf monkey (Presbytis melalophos)
Binturong	Canivora	Viverridae	**Vulnerable (2016):** Binturong (*Arctictis binturong*)

(continued) Table 4.02 Animals in the seed dispersal network of Belum

Animal	**Order**	**Family**	**Genus / Species (IUCN)**
Civets	Canivora	Viverridae	**Least concerned (2015):** Small Indian civet (*Viverricula indica*), Masked palm civet (*Paguma larvata*), Common palm civet *(Paradoxurus hermaphroditus),* Small-tooth palm civet (*Arctogalidia trivirgata*).
Colugo	Dermoptera	Cynocephalidae	**Least concerned (2008):** *Galeopterus variegatus*
Malayan sun bear	Canivora	Ursidae	**Vulnerable (2016):** *Helarctos malayanus*
<u>Terrestrial mammals (except rodents)</u>			
Asian elephant	Elephas	Maximum	**Endangered (2008)**
Gaur	Artiodactyla	Bovidae	**Vulnerable (2016):** *Bos gaurus*
Mousedeers	Artiodactyla	Tragulidae	**Least concerned (2014):** Lesser Oriental Chevrotain (*Tragulus kanchil),* Greater Oriental Chevrotain (*Tragulus napu)*
Southern red muntjac	Artiodactyla	Cervidae	**Least concerned (2015):** *Muntiacus muntjac*
Sambar deer	Artiodactyla	Cervidae	**Vulnerable (2014):** *Rusa unicolor*
Malayan Tapir	Perissodactyla	Tapiridae	**Endangered (2014):** *Tapirus indicus*
Wild boar	Artiodactyla	Suidae	**Least concerned (2018):** *Sus scrofa*
Human	Primates	Hominidae	**Least concerned (2008):** *Homo sapiens*
Macaques	Primates	Cercopithecidae	**Vulnerable (2008):** Southern pig-tailed macaque (*Macaca nemestrina*) **Least concerned (2008):** Nicobar crab-eating macaque (*macaca fascicularis*)

(continued) Table 4.02 Animals in the seed dispersal network of Belum

Animal	Order	Family	Genus / Species (IUCN)
Rodents			
Squirrels	Rodentia	Sciurinae	**Examples of species in Belum:** Black giant squirrel (*Ratufa bicolor, 2016*), **Near threatened:** Pale giant squirrel (*Ratufa affinis, 2016*), **Least concern (2016):** Plantain squirrel (*Callosiurus notatus, 2016),* Prevost's squirrel (*Callosciurus prevostii, 2016),* Black-banded squirrel (*Callosciurus nigrovittatus, 2017),* Pallas's squirrel (*Callosciurus erythraeus*, 2016), Slender squirrel (*Sundasciurus tenuis*, 2016), Low's squirrel (*Sundasciurus lowii, 2016),* Himalayan striped squirrel (*Tamiops macclellandii*, 2016), Three-striped ground squirrel (Ratnam et al., 1995) **Other possible species:** Grey-bellied squirrel (*Callosciurus caniceps),* Horse-tailed squirrel (*Sundasciurus hippurus*), Red-cheeked squirrel (*Dremomys rufigenis*), Shrew-faced ground squirrel (Rhinosciurus laticaudatus) (Francis, 2008)
Flying Squirrels	Rodentia	Sciurinae	**Least concerned (2016):** Red-Cheeked Flying Squirrel (*Hylopetes spadiceus*), Horsfield's Flying Squirrel (*Iomys horsfieldii*), Spotted Giant Flying Squirrel (*Petaurista elegans*), Red Giant Flying Squirrel (*Petaurista petaurista*) **Vulnerable**: Whiskered Flying Squirrel (*Petinomys genibarbis*) **Data deficient:** Black Flying Squirrel (*Aeromys tephromelas*)
Porcupines	Rodentia	Hystricidae	**Least concerned (2016):** Malayan Porcupine (*Hystrix brachyura),* Asiatic brush-tailed porcupine (*Atherurus macrourus*), long-tailed porcupine (*Trichys fasciulata*)
Rats	Rodentia	Muridae	**Examples of species in Belum** **Least concerned (2016):** Polynesian rat (*Rattus exulans*), House rat (*Rattus rattus*), House rat (*Rattus diardi*), Malaysian wood rat (*Rattus tiomanicus),* Müller's rat (*Sundamys muelleri*), long-tailed giant rat (*Leopoldamys sabanus*), Indomalayan pencil-tailed tree mouse *(Chiropodomys gliroides),* Indomalayan Maxomys (*Maxomys surifer*), Sundaic Arboreal Niviventer (*Niviventer cremoriventer*), Bower's White-toothed rat *(Berylmys bowersi)*

Vulnerable (2016):
Whitehead's Sundaic Maxomys (*Maxomys whiteheadi)* (Ratnam et al., 1995; Nur Aida et al., 2008)
Other possible species:
Pacific rat (*Rattus exulans*), Ricefield rat (*Rattus argentiventer*), Norway rat (*Rattus norvegicus*), Müller's rat (*Sundamys muelleri*), Malayan wolly tree rat (*Pithecheir parvus*), Grey tree rat (*Lenothrix canus*), Indomalayan Niviventer (*Niviventer fulvescens*), Rajah maxomys (*Maxomys rajah*), Asian house mouse (*Mus musculus*), excluding bamboo rats (*Rhizomys spp.*) (Francis, 2008)

Interviews – I interviewed twelve pairs of local indigenous people from six villages, and three additional single-person interviews with individuals familiar with plant-animal interactions and the sampled fruits, including two field assistants. One group's answer was forfeited as one of the interviewees appeared over-confident, resulting in over-represented interactions. A total of 14 sets of answers were gathered. The participants in each pair were encouraged to discuss their experiences with each other (Appendix Fig. A4.17). Interviews were visually oriented (Fig. 4.02).

I presented to the interviewees an image(s) of the focal animal and requested for them to select plants eaten by the animal from a plant booklet provided. Each page of the booklet consisted of photographs of fruits and seeds printed as close as possible to their actual sizes, and leaves (when available) of a sampled plant species. All 164 fruits in the sample were included (Appendix Table A4.1). To facilitate the thinking process, fruits were ordered from the smallest to the largest size. To reduce biases, the pages were flipped individually. When a plant was selected, the following questions were presented along with Fig. 4.02:

1) Can you identify from here the seed treatment of the fruit consumed by the animal?
2) Is this a preferred food plant (interpreted as a commonly observed interaction)?

I explained that seeds in treatment one to three were found in faecal material, treatment four were regurgitated, treatment five were seeds targeted as food (not the pulp) and hoarded by the animals, treatment six as seeds targeted as food but not hoarded, and treatment seven as the pulp targeted as food and the seeds carried away from the parent plant (but not swallowed). I requested the participants to indicate whether their answers were based on personal observation or passed-on knowledge. When I explained to the participants to exclude logical deductions, I found that they do not have a term for 'logic' in their language. The closest term was 'no guessing'. Since their knowledge is accumulated by memory with no written records, I expect that the interactions gathered to be mixed with personal logical deductions.

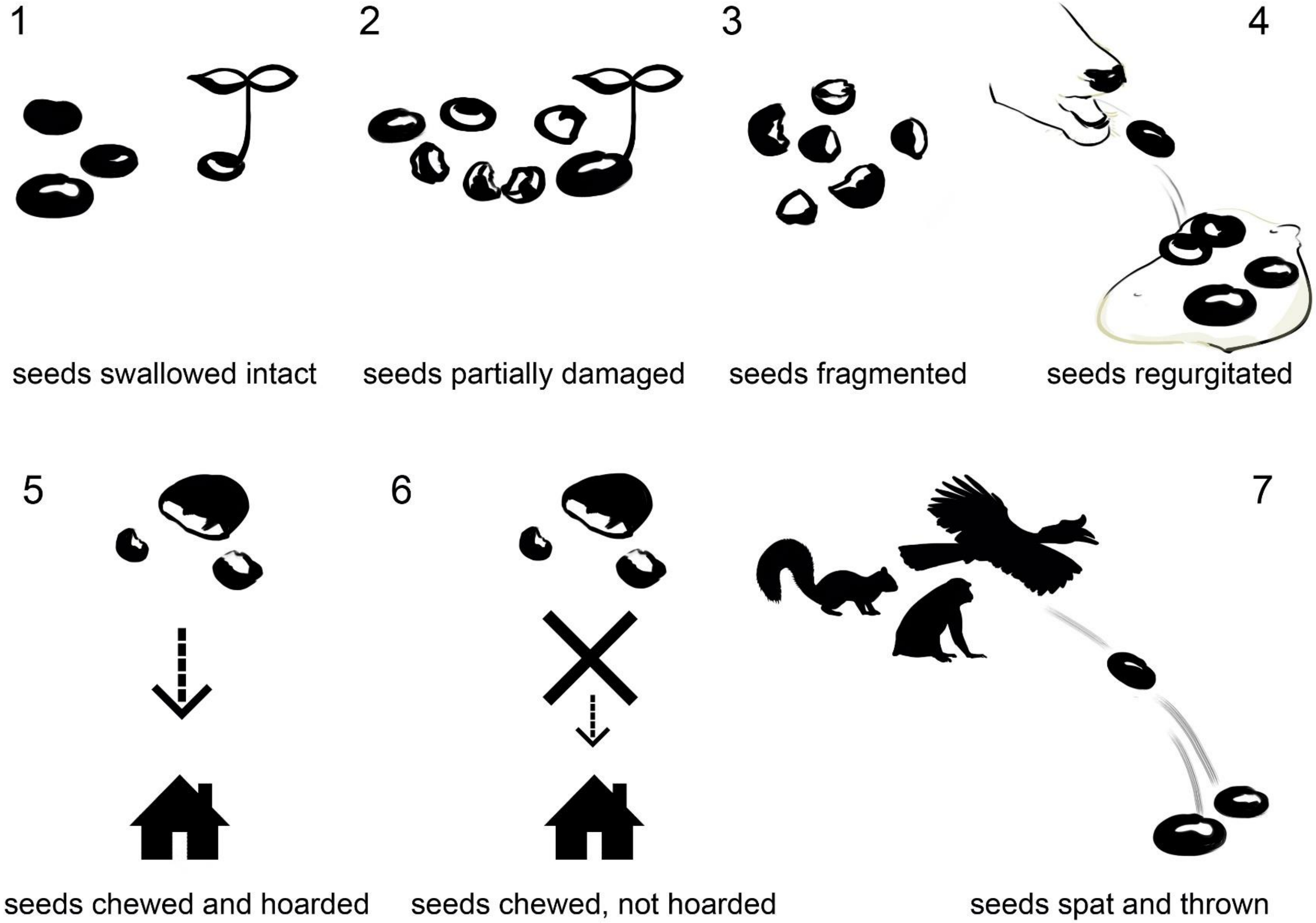


Figure 4.02 Different seed treatment by animals. 1 and 2 were grouped as 'seeds defecated intact', and 3 was assigned as 'seeds fragmented'. It was necessary to include 2 to avoid the confusion between seed treatment 1 and 3.

Assignment of Seed Dispersal Interactions

Combining LEK with published records – The use of LEK allowed us to collect dispersal interactions that would have been impossible to observe over a short period. However, this method has concerns that I had to address, and I improved the dataset with published information. A summary of the decisions was shown in Fig. 4.03 and Table 4.05.

Criteria for Using LEK – Although I carried out 14 interviews in total, only seven interviews were gathered for most birds. To prevent biases, I inferred LEK only from **seven** groups (six groups for nuthatches and the Malayan flying fox) with the highest records of interactions for each animal. The criteria for the utilization of LEK and published records are summarised in Table 4.03 and examples are provided in Table 4.04.

Table 4.03 Criteria for using LEK. Examples are shown in Table 4.04

Frugivory	i) Identified by at least two LEK groups, **or** ii) 1 LEK group + transect evidence (interaction quadrat, camera traps, regurgitated or defecated seeds found), **or** iii) 1 published record indicating seed dispersal information of the plant genus
Dispersal/ Seed predation	Identified by at least two LEK interviewee groups **or** 1 LEK group + 1 transect evidence **or** 1 published record indicating seed dispersal information of the plant genus. iv) In seed predation, published ref. overrides LEK information *In fruit genera where fruit sizes are highly varied (e.g. *Diospyros and Garcinia spp.*), fruit or seed sizes were matched to infer dispersal, provided that the information was available. See details in section Published Records, point 2.

Table 4.04: Decision for seed treatment assignment using LEK. Highlighted: treatment indicated.

Criteria	**Fruit name**	**Treatment observed (LEK group)**							**Other evidence**	**Decision**
		1	2	3	4	5	6	7		
i	*Vatica* sp. 1	**7**	0	0	0	**1**	0	0		LEK used, treatment follow 7
ii	*Callophyllum macrocarpum*	0	**1**	0	0	0	0	0	Camera trap eating	LEK used, treatment follow 1
iii	*Turpinia* sp. 1	0	0	0	0	0	0	0	Ref: seed dispersed	Assigned treatment according to upper limit (explained in next section)
iv	*Combretum* sp. 1	**1**	0	**2**	0	**3**	0	0	Ref: predation	LEK used, assigned seed predation
	*Perpir**	0	0	0	0	**1**	0	0	Ref: consumed	Reject

Seed treatments examples provided: (1)seeds swallowed intact, (7) seeds spat and thrown.

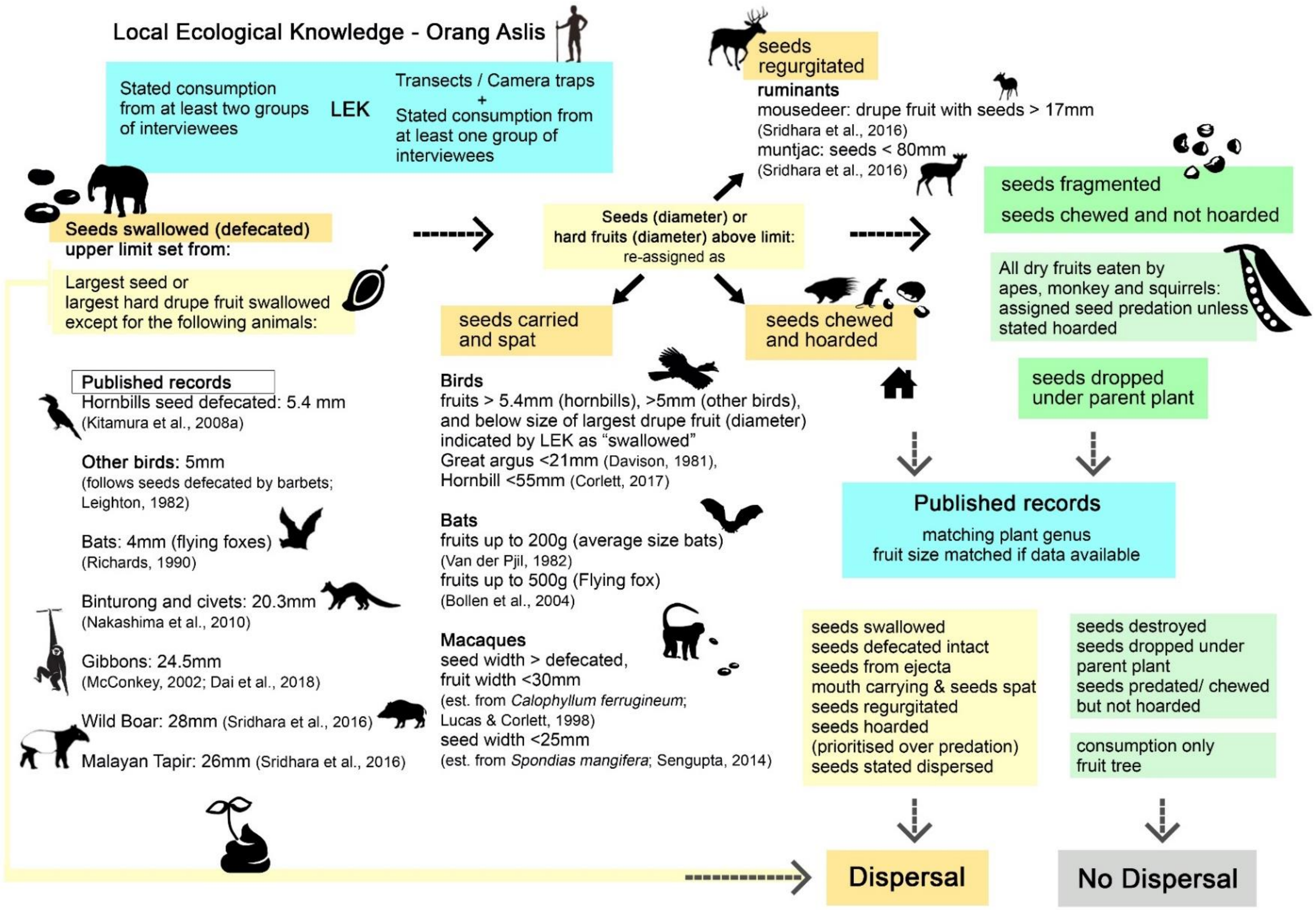


Figure 4.03 Process of determining seed dispersal from LEK and published records. Full details are explained in the next section: Assignment of Seed Dispersal Interactions.

Table 4.05 Seed dispersal limits set from LEK or published records in different animals

Birds	**Seeds swallowed & defecated** **upper limit:** **hornbills[1]:** 5.4mm **others[2]:** 5mm (follows seed length defecated by barbets — wide gapes) 1. Kitamura et al., 2008a 2. Leighton, 1982 3. Read descriptions about birds 4. Davison, 1981 5. Corlett, 2017	**Seeds carried and spat** **lower limit:** as swallowed **upper limit:** 'largest indehiscent drupe fruit' or 'largest dehiscent-fruit seed' indicated swallowed[3] **Great argus[4]**: 21mm **hornbills[5]:** 55mm	**Seeds dropped** > seeds carried and spat limit **Seed predation** LEK or published records
Bats	**Seeds swallowed & defecated** From local info., only *Ficus* sp. seeds are defecated intact. **Malayan flying fox[6]**: 4mm 6. Richards, 1990 7. Van der Pijl, 1982 8. Bollen et al., 2004	**Mouth-carrying of fruits and seeds spat** **bats[7]:** Fruits up to 200g, and seeds of *Artocarpus* spp. **Malayan flying fox[8]:** Fruits up to 500g, and seeds of *Artocarpus* spp. Note: *Artocarpus* spp. are aggregate fruits. Fleshy fruit bulbs of fruit can be carried by bats.	
Macaques	**Seeds swallowed & defecated** **upper limit:** the size of the largest seed 'swallowed'[3] (LEK) 9. Lucas & Corlett, 1998 10. Sengupta, 2014	**Seeds carried in cheek pouch and spat** fruit width above 30mm[9], seed width above 25mm[10].	**Seed predation** LEK or published records **Seeds dropped** Fruits width ≥ 30mm[9] or seed width above 25mm[10].
Langurs	**Seeds swallowed & defecated** **upper limit:** the size of the largest seed 'swallowed'[3] (LEK)	**Seeds dropped** above swallowing limit	**Seed predation** LEK or published records
Human	No seeds swallowed & defecated	**Seeds carried and spat** LEK	**Seed predation** LEK or published records
Other animals	**Seeds swallowed & defecated** **upper limit:** the size of the largest seed 'swallowed'[3] (LEK) **gibbons[10]**: 24.5mm **binturong and civets[11]**: 20.3mm **wild boar[12]**: 28mm **Malayan tapir[12]**: 26mm 10 McConkey 2002; Dai et al., 2018 11. Nakashima et al., 2010 12. Sridhara et al., 2016	**Seeds regurgitated** LEK or published records **mousedeer[12]**: drupe fruits with seeds > 17mm **Southern red muntjac[12]**: seeds <80mm	**Seed predation/ destroyed/ hoarding** LEK or published records **Seeds dropped** above swallowing limit

Assignment of Seed Dispersal Interactions

1) **Seed dispersal by birds:** I found most Orang Asli were not particularly familiar with bird seed-dispersal interactions, and the surveys were weaker for compiling bird-related interactions than mammal interactions.

   During the interviews, I explained that treatments one to three were found in faecal material and treatment seven was meant for seeds carried away from the parent plant (Fig. 4.01). However, I found that it can be difficult to strictly discern the differences as birds handled seeds in multiple ways. Birds can disperse seeds by a) carrying seeds in their beaks which are subsequently spat, b) storing of seeds in their gular pouch or oesophagus which is subsequently regurgitated (e.g. hornbills), c) vomiting of seeds in the form of pellets that were processed in the stomach, d) defecating seeds that are sometimes difficult to differentiate from pellets, and e)hoarding of seeds. When fruits are too large to fit a bird's beak, birds often peck on fruits, dropping seeds directly under the parent plant (Brockelman, 1982).

   In practice, it would be more straightforward to exclude interactions of birds that pecked on fruits without swallowing the seed. When birds were observed removing fruits from trees, it is difficult to judge the final seed treatment unless the observers often see such regurgitated seeds or vomited pellets along the trails or under some resting roosts. Thus, the chance of receiving incorrect information for bird dispersal is high. This posed a problem as I allocated different weights to defecated and regurgitated seeds to the network (further described in the interaction matrix). Since hornbills are larger and are hunted (Bartholomew, 2017), they were more commonly observed by the Orang Asli and the information of seeds spat is likely reliable.

   The interactions that I gathered of seeds swallowed by birds through LEK included a wide range of fruit and seed sizes. From reviews, however, I found seeds defecated by birds with large gape sizes to be small. For example, barbets defecated seeds not larger than 5mm (Leighton, 1982), while hornbills defecated seeds not larger than 5.4mm (Kitamura, 2008a). Likely, many seeds assumed as swallowed and defecated by birds could be spat, regurgitated, or vomited.

   Solution: I thus use 5mm as the size limits of seeds defecated by all birds, and 5.4mm for seed sizes defecated by hornbills. Although there were differences between mouth-carrying, regurgitation, and vomiting, I was unable to differentiate these seed treatments. **I re-assigned** all seeds above 5.4mm(hornbills) and 5mm (other birds) **from 'seeds swallowed' to 'seeds carried and spat' by birds. I reserved the description of 'regurgitation' to the regurgitation of ingesta for ruminants in this study**.

As explained earlier, 'seed dropped (directly under a parent plant)' interactions could be misidentified as 'seeds spat'. Hence, I need to 1) identify an upper limit for seeds that could be carried by each bird taxon; and 2) to apply this limit on the dataset of each bird species, removing plants that were too large to be carried. Apart from sizes, I also need to consider the traits of fruits consumed. Fleshy indehiscent fruits can be eaten whole but not dehiscent fruits that are often protected by hard outer covering. As compared to a berry, the size of a drupe fruit would serve as a better reference for demarcating the limit of seeds that could be carried away by birds in their beaks. Such fruit often has a large seed surrounded by a layer of thin flesh.

Solution: To set an upper size limit for seeds that could be carried away by birds in their beaks, I hence used the size of either the 'largest indehiscent drupe fruit' or the 'largest dehiscent seed' originally indicated as 'swallowed' by at least two LEK interviews (Table 4.06). This limit was applied to the dataset. Seed sizes above this limit will be assigned as seeds dropped.

Table 4.06: Example of decision for the upper limit of 'seeds carried and spat' by birds. Seed treatment 1: seeds indicated as swallowed intact. Seed treatment 7: seeds indicated as spate and thrown. Highlighted: LEK with seed treatment 1. Bold: Interviews that provided a treatment for the pairwise interaction.

Fruit name	**Fruit type (piercing)**	**Treatment observed (LEK group)**							**Fruit dia. (mm)**	**Seed dia. (mm)**	**Decision for using measurement as limit**
		1	2	3	4	5	6	7			
Prunus sp. 1	**Indehiscent** fleshy **drupe** (easy)	**1**	0	0	**1**	**7**	0	0	**14.4**	10.8	Use fruit size as seeds carried and spat limit
Neoscortechinia sp. 1	**dehiscent** dry follicle (difficult)	**7**	0	**7**	**0**	**1**	**1**	0	22.5	**16.9**	Used seed size as seeds carried and spat limit
Fabaceae sp.	dehiscent dry pod	**7**	0	0	**7**	**1**	**0**	0	70.1	**26.8**	Rejected as only 1 group indicated treatment 1

With this method, I found the sizes of seeds close to some examples I found in published papers. For example, the largest seed I assigned as 'carried and spat' by bulbuls was 12.5mm due to a similar genus (*Polyalthia sp.*) recorded to be dispersed bulbuls (Kitamura, 2002); otherwise, data solely from LEK indicated 8.8mm. Corlett (2017) estimated bulbuls can regurgitate seeds around 10mm. This method has its limitations and can be further improved by doing a more thorough review (e.g. for hoarding) of seed dispersal by different bird species. No Orang Asli had observed hoarding of seeds by birds.

2) **Seed dispersal by bats:** Information provided by LEK matched published records well. Only *Ficus* species were indicated as being swallowed and defecated by bats (seed sizes around 1mm). Published literature also showed that bats defecate small seeds, most of which belong to *Ficus* spp. (up to 4mm; Corlett, 1998). Albeit infrequently, fruit bats such as *Cynopterus brachyotis* are known to carry fruits 50 to 70 m away from fruiting trees (Phua & Corlett, 1989; Tan et al., 2000) and these fruits can be more than their body weight. Unlike the smaller bats, large bats such as *Pteropus giganteus* often process fruits 'in situ' (Mahandran & Nathan, 2018). When a tree has large fruit crops, territorial bats will fight over feeding territories. To avoid aggression, they sometimes carry fruits away to neighbouring trees or temporary feeding roosts (Richards, 1990; Tang et al., 2012; Corlett, 2014). Rare long-distance seed dispersal of several kilometres had been previously recorded (Mahandran et al., 2018).

   Assignment: I assigned seeds less than 4mm as 'swallowed and defecated' by bats (Corlett, 1998). I also assigned fruits up to 200g as 'seeds carried and spat' (mouth-carrying) by average-size bats, and fruits up to 500g by the Malayan flying fox. In this study, there were only six fruits that were heavier than 200g, and two above 500g. Of these six fruits, three were *Artocarpus* spp. These fruits consisted of fleshy bulbs with small seeds (seed width 8.8 to 10.6 mm) and were assigned as fruits dispersed by all bats.

3) **Seed dispersal by macaques:** I gathered valuable information on seed treatment by macaques through LEK. Due to the varied ways in which macaques disperse seeds, validations of the interactions were needed.

   Seeds of fruits consumed by macaques can be a) swallowed, b) transported away from the plant in their cheek pouches before seeds are spat individually, c) predated or d) dropped directly under the fruiting plant (Corlett & Lucas, 1990; Albert et al., 2013).

   Solution: I estimated fruits spat by macaques to be less than 30mm and seeds spat to be less than 25mm (referring to *Calophyllum ferrugineum* fruit: Lucas & Corlett, 1998; *Spondias mangifera* seed: Sengupta, 2014). I thus re-assigned all seed sizes above 25mm as 'seeds dropped'. Except for *Artocarpus* species, I also re-assigned 'indehiscent fruits that were difficult to pierce' with fruit sizes >30mm as 'seeds dropped'. 'Seed predation' followed information provided by LEK or published references.

4) **Seed dispersal by gibbons:** Contrary to existing studies of gibbons, seed treatments gathered from LEK indicated high levels of seed predation by gibbons. There is a possibility of misinterpretation of the feeding habits of gibbons, because some of the trees they use as resting sites have fruit and seeds consumed by other monkeys.
   Available studies of gibbons provided comprehensive information on gibbon diet and seed dispersal (e.g. McConkey, 2000; Kitamura, 2002; Dai et al., 2018). According to studies from similar habitats, seed predation by gibbons is uncommon; such that around 9% of their diet in Sundaic forests is seeds and unripe fruit (McConkey et al., 2002). In LEK, several seeds were indicated to be destroyed by gibbons, including several species from the dry-fruited Fabaceae, Sterculiaceae families, and Dipterocarpaceae family. There is a possibility that gibbons had been predating on seeds in periods when food was scarce. There is also a possibility that some dry-fruited species were misidentified as food of gibbons. Trees from the Fabaceae, Sterculiaceae, and Dipterocarpaceae family are tall canopy trees typically used as a night-time resting site by gibbons (Reichard, 1998; Phoonjampa et al., 2010). Pig-tailed Macaques (*Macaca nemestrina*) frequently used dipterocarps as sleeping trees. Although the monkeys and the apes avoided contact, they may rest in the same tree when the other monkeys/apes are not around (Reichard, 1998). Additionally, both species sometimes exploit similar fruits and their teeth marks could have been mixed up, leading to wrong conclusions of gibbons feeding. More studies of gibbons and monkeys are needed to validate their seed dispersal interactions.
   Solution: Except for two Sterculiaceae species with seeds that were relatively soft, all dry fruits identified as consumed by gibbons from LEK were removed as examples of 'seed predation' since there are no published records that these fruits feature in gibbon diets. Fruits identified by LEK as being gibbon-consumed with seed sizes below 24.5mm were assigned as 'seeds swallowed' (24.5mm from Dai et al.; 21mm from McConkey 2000), and seed sizes 24.5mm or above were assigned as 'seed dropped'.

5) **Handling of hard fruits by monkeys or apes:** Some hard and difficult to handle fruits were indicated as swallowed by monkeys or apes.
   Solution: Indehiscent fruits that were too hard (overall structure) to process were excluded from swallowing by monkeys and gibbons. There were few such fruits in the collection.

6) **'Seed dropped' limits for all taxonomic groups**: There is a variation of seed sizes indicated as dispersed by different animals. Some were above the sizes of existing studies. Although these plants represent a small proportion of the interactions that I gathered for the matrix, I saw the need to set sensible minimum and maximum limits to the size of 'seeds dropped'.

Solution: For well-studied animals, I followed the maximum seed-swallowed sizes (e.g. 20.3mm for civets; Nakashima et al., 2010) or fruits dispersed sizes (e.g. 500g for the Malayan flying fox; Bollen et al., 2004) as recorded by the different authors (see next section for further explanation). For animals without established studies, I set limits using:

i) the 'largest indehiscent drupe fruit' or 'largest dehiscent drupe seed' originally indicated as swallowed by at least two LEK interviews for birds, whichever is larger.
ii) the 'largest seed' indicated as swallowed by at least two LEK interviews for other animals.

7) **Regurgitation limits for ruminants:** Seeds below the sizes recorded in published studies were indicated as 'seed dropped' instead of 'regurgitated'.
Ruminants include the Tragulidae — Lesser Oriental chevrotain (*Tragulus kanchil)* and Greater Oriental chevrotain (*Tragulus napu)*, Cervidae — Southern red muntjac (*Muntiacus muntjac*) and Bovidae — gaur (*Bos gaurus*). Ruminants have strong molars that destroy seeds during mastication (Bodmer, 1991). Large stony seeds that are protected by hard coverings, usually belonging to drupe fruits, may survive this chewing effect and are subsequently swallowed (Chen et al., 2001; Prasad et al., 2006). As foregut fermenters with three to four stomach chambers, ruminants constrain the size of food particles passing through the forestomach. Small seeds (usually <1mm) that could pass through are defecated intact while the larger hard seeds regurgitated several hours later (Mouissie et al., 2005; Prasad et al., 2006).
Solution: A regurgitation limit is set for mousedeer at 17mm and muntjac at 80mm (reference Sridhara et al., 2016). Only drupe fruits with medium to hard seeds were re-assigned from dropped to regurgitated seeds. There are no available studies of seed dispersal by gaur. Only two plant species — *Spondias cf. pinnata* and *Irvingia malayana* were indicated as regurgitated by one LEK interview; and I assigned these as regurgitated by gaur.

8) **Disagreement in seed treatments from LEK:** It was common for different respondents to disagree in the seed treatments they assigned to interactions during the LEK interviews. For example, one interview indicating treatment 1 and another indicating treatment 7.
Solution: I took a conservative approach in finalizing the seed treatment by selecting the treatment that was least likely to result in effective dispersal (Table 4.07). For example, if a group selected treatment 5 and a group selected treatment 6, the final seed treatment assignment would be treatment 6 (Table 4.08). The exception to this was for regurgitation where thrown seeds were difficult to differentiate from regurgitated seeds (see point 7), Treatments were also assigned as seed predation if this was recorded in published records.

Table 4.07: Conservative decision of seed treatment selection. Treatment 1 and 2 represented effective seed dispersal. Treatment 4, 5, and 7 would subsequently be assigned a lower weightage and Treatment 3 and 6 were undispersed seeds.

→ **Conservative Decision**

Treatment 1 and 2	**Treatment 4, 7 and 5**	**Treatment 3 and 6**
Seeds swallowed and defecated intact Seeds partially intact and partially damaged	Seeds spat and thrown Seeds chewed and hoarded	Seeds fragmented Seeds chewed but not hoarded (seeds predated)

Table 4.08: Example of finalising decision of seed treatment

Fruit name	**Treatment observed (LEK group)**							**Decision for using measurement as limit**	**Implication**
	1	2	3	4	5	6	7		
Neoscortechinia sp. 1	0	0	0	0	**5**	**5**	0	Assigned treatment 5 (hoarding)	Considered as dispersed
Fabaceae sp. 1	0	0	0	**5**	**6**	0	0	Assigned treatment 6 (seed predation)	Considered as non-dispersed

9) **Seed dispersed not recorded by LEK but found in published records:** I found less than 1% (38 out of 5576 possible combinations) indicated as dispersed plants (genus) from published records, but not as dispersed plants by LEK.
Solution: These could be interactions that were not observed by the Orang Asli. I assigned these interactions as dispersal (Table 4.03). Plants with only 'fruit consumption' indicated in published records were excluded.

(IV) Published Records

I used published literature to improve the information I obtained from LEK. I searched the web using *Google Scholar* and a combination of words: '*Triomma malaccensis* parrots disperse fruit' and '*Triomma malaccensis* fruits seeds disperse animal'. The plant species were included when available. I found more than 600 references from google scholar across all combinations. Only 112 papers/books provided matching interactions of similar plant genus. 1389 matching interactions were used to improve the dataset, of which, 359 had two references. Interactions with more than two references were excluded from the reference list. Similar to LEK, I faced another set of challenges with the published literature.

1) **Dependent on the aims of the studies, most literature did not provide precise information on seed treatment.**
Solution: I extracted further information (e.g., observation, local information, in faces, from ejecta, etc.) to help with the final decision of categorizing the seed treatments (Table 4.09). In

the datasheet, final treatment for dispersed seeds was standardized with a short description such as 'seeds defecated', 'seed from ejecta', 'mouth-carrying', 'stated dispersal only' etc.

Table 4.09 Utilisation of published records and the extraction of seed treatment information. Further information could be extracted from methods or other paragraphs.

Author	Plant Species	Animal Species	Described as	Further Information	Final treatment
Fredriksson et al.	*Monocarpia kalimantanensis*	*Helarctos malayanus*	fruits consumed	in faecal	defecated seeds
Fredriksson et al.	*Syzygium tawahense*	*Helarctos malayanus*	fruits consumed	observation	fruits consumed
Kitamura	*Diospyros glandulosa*	*Ursus malayanus*	seeds dropped under parent plant		seeds dropped under the parent plant
Kitamura	*Ficus altissima*	*Ursus malayanus*	stated disperser		stated dispersal

2) **36% provided only consumption but not seed treatment information:** Information of consumption allowed us to visualise how much of LEK information overlapped with published records but did not add to the value of the assignment of a seed-dispersal decision. **Solution:** I did not assign these interactions as dispersed species (Table 4.09).

3) **Several plant species in the collection were not common in other studies.**

It was impossible to validate interactions at a species level and determine if fruits were similar. Matching fruit and seed measurements at the genus level served as the next best option to reference dispersal. However, such measurements are limited in the literature and it would be too time-consuming to obtain all measurements.
Solution: I matched interactions at the genus level. For genera that had species with very variable fruit sizes (e.g., *Diospyros* and *Garcinia* species), I referenced dispersal more carefully by matching the seed width provided by published records to the fruit collection. For example, if a published record showed the dispersed seed was 10mm, plants with seeds much larger than this from the collection will not be assigned dispersal (from the use of published records). I also matched measurements for a few large-fruited or obviously size-variable species. Most other genera were not matched with measurements in detail.

Interaction Matrix

I created two sets of interaction matrix – one representing frugivory, another representing seed-dispersal. Only the seed-dispersal network structure will be discussed in detail.

***Weighted network* –** Network weights are important to detecting modules more accurately, helping to prevent over-estimating the strength of rare interactions and underestimating the importance of highly interactive species (Newman, 2004; Dormann & Strauss, 2013). I built a weighted network for seed dispersal considering the effectiveness of dispersal, by multiplying the frequency of observations (quantity) to a factor representing different modes of dispersal (quality). The frequency of observations was obtained from LEK of how commonly an interaction is observed. For example, when 4 out of 7 interviewed groups indicated 'yes' to common observation, a weight of 0.57 (4/7) was applied. When no group indicated 'yes' to common observation, a minimum weight of 0.1 was applied. Three factors were assigned to the different modes of dispersal (i) 1 to seeds swallowed and defecated, (ii) 0.25 to seeds hoarded, and (ii) 0.5 to other modes of dispersal such as seeds carried and spat by birds, regurgitation by ruminants, mouth carrying by bats and seeds spat by macaques. This quality component considers the likelihood of germination success and fitness with increased dispersal distance away from a parent plant (Janzen, 1970). Since this approach is not common (multi-disciplinary and weighted), I checked the degree distribution (Table A4.19) for the expected frequency of usual seed dispersal networks, i.e., a truncated power-law distribution (Bascompte & Jordano, 2014).

***Notes on dispersal effectiveness* –** I distinguished these different modes of dispersal in the network by applying a numerical value that reflects the "dispersal effectiveness" of the mode. Ideally, effective dispersal ensures successful reproduction, measured as the number of new adults produced by the dispersal activities of a disperser. Empirically, effectiveness can be projected as the quantity of seeds dispersed as a product of the probability a dispersed seed can grow into a reproductive adult, i.e., effectiveness = quantity x quality (Schupp, 1993). The quantity of seeds dispersed can be represented by (1) the 'number of visits made' by a disperser considering the abundance, diet and reliability of visitation by the disperser; and (2) the 'number of seeds dispersed per visit' taking into account the number of seeds handled, and the probability of dispersing a handled seed. The quality of seed dispersal can be presented by (1) the 'quality of treatment' considering if seeds are defecated intact and the success or rate of germination; and (2) the 'quality of deposition' that is dependent on movement patterns (a. habitat and microsite selection; b. rate and directionality of movement) and deposition patterns (a. rate and pattern of deposition; b. seed-diet mixing). Most studies, however, are unable to measure both aspects of quantity and quality fully (Schupp, 1993). The effectiveness of seed dispersal in this network is thus a very simplified representation of the dispersal effectiveness of the system.

Notes on quality of dispersal used in network – I generalised different modes of dispersal in the network, dividing them into three main groups of dispersal, i.e. (1) seeds defecated, (2) seeds hoarded, and (3) other modes of dispersal (seeds carried and spat, regurgitation by ruminants, mouth carrying, and seeds spat). As described earlier, the 'quality of treatment' considers if seeds are defecated intact and the success or rate of germination.

I assigned the highest factor (of 1) to the first group of seed dispersal mode, i.e., seeds swallowed and defecated intact. Seeds ingested and defecated intact are freed from fruit pulp, especially in lipid-rich fruits, increasing the success of germination (Broschat & Donselman, 1987; Traveset et al., 2002). While seeds that are cleaned and spat or regurgitated also benefit from having the seeds depulped, seeds swallowed have an additional benefit of being transported further away due to longer gut retention times that increase seed dispersal distances (Schupp, 1993, Guttal et al., 2011). Closer to the parent plant, many seeds dispersed by animals such as primates, are subject to high levels of seed predation (Janzen, 1970). Although this could lead to successful secondary seed dispersal (Forget & Milleron, 1991; Hoshizaki et al., 1997) which is also important, the pressure of seed predation is comparatively higher than seeds dispersed further away. Additionally, plants dispersed further away are also subjected to lower effects of density-dependent mortality (e.g. Penfold & Lamb, 1999). The niche partitioning hypothesis predicts that the overlapping niches of conspecifics result in a higher competition of similar resources (e.g. nutrients); differentiation in the main niche is thus needed to avoid this competition (MacArthur, 1958). Co-existence is promoted when seeds are dispersed away from their conspecific.

I assigned a factor of 0.25 to seed hoarding. In seed dispersal, hoarding of seeds also helps transport seeds away from the parent plant. Scatter-hoarding of seeds in shallow caches results in lower recovery success as compared to larder-hoarding of seeds in deeper caches (Smith & Reichman, 1984; Vander wall, 1990; Jansen & Forget, 2001). The difference in caching strategies and recovery success by animals results in higher germination success for scatter-hoarded seeds. Amongst animals that hoard seeds (e.g. Jays, woodpeckers, ants), hoarding by rodents is more commonly represented in this study. A lower factor was assigned as many cached seeds are often recovered, and germination rates are lower (Jansen et al., 2012). Additionally, the seed dispersal distance of rodents is comparatively lesser than other modes of dispersal (e.g. Yasuda et al., 2000; Li & Zhang, 2003). Asian elephants may ingest and disperse seeds up to 3.5 km (Campos-Arceiz et al., 2008) or even over 10km (Sekar et al., 2015).

I assigned a factor of 0.5 to other modes of seed-dispersal. Macaques may carry and spit seeds up to several hundred metres (Albert et al., 2013). Long-distance dispersal of seeds has been found for birds that defecate or regurgitate seeds (Proctor, 1968), and ruminants can retain seeds up to 72hours before regurgitating them (Prasad et al., 2006). 'Other modes of seed dispersal' seem to have an overall advantage in dispersal distance over hoarding but appear less promising overall as compared to the dispersal fitness advantage attached to 'ingested seeds' as previously described. Although this method is a simplified representation of seed dispersal effectiveness, it nonetheless allowed for a sensible setup of a weighted network, to help address the dependencies of seed dispersal on different animals more clearly in this system.

Analysis of bipartite networks

I relied on Microsoft excel, version 2004, and the R statistical environment 3.5.3 (R Core Team, 2019) for data set up and analysis. I carried out network visualization with the *ggplot 2* (Wicham, 2016), *igraph* (Csardi & Nepusz, 2006), and the *bipartite* (Dormann et al., 2008, 2009; Dorman 2011) packages. As the assignment of modules is based on an optimization process, I computed the modules 50 times to decide on the final modules representing the network. To summarise the network topologies, I calculated indices at both network, group (higher animals, lower plants), and species level. I compared the network indices to the Patefield null model (details of this method can be found in Dormann et al., 2009). The following indices are used to describe the network properties:

At Network Level

Modularity describes the likelihood of the module's make-up and clustering in a network, calculated as (Barber, 2007):

$$M = \sum_{i=1}^{n} \frac{e_i}{L} - \frac{d_i^P}{L}\frac{d_i^A}{L}$$

Where n is the number of modules, e_i is the number of interactions within module *i*, *L* is the total number of interactions in the network, d_i^P is the sum of degrees for plants in module *i* and d_i^A the sum of degrees of nodes in module *i* for animals. In contrast to a random network structure (M=0), a modular network has M >0, ranging up to 1. Tropical networks reflect similar modularity (mean 0.36; min. 0.1, max 0.7), with no significant differences between biogeographic regions (Dugger et al., 2018). High modularity prevents extinction cascades (Olesen et al., 2007).

Weighted Connectance is the observed proportion of possible links in a network. This index responds to non-interacting species. High network connectance maintains community stability (Jordano, 1987).

$$connectance = \frac{linkage\ density}{number\ of\ species\ in\ network}$$

Weighted NODF (nestedness metric based on the overlap and decreasing fill) represents the amount of hierarchical structure in a network. This index takes into account weights, measuring nestedness with a sequential approach, quantifying if a sequence of columns/rows exhibits decreasing marginal totals of richness. It is proposed by Almeida-Neto et al. (2011), correcting for matrix fill and matrix dimensions. It ranges between 0 (non-nestedness) and 100 (perfect nestedness). Highly nested networks have low-degree nodes interacting with high-degree nodes that in turn interact with other nodes of high degree.

At plant and animal community level

The **mean number of shared partners** is the average number of shared partners of a node.

Generality HL is the effective mean number of links per animal mutualist.
Vulnerability LL is the effective mean number of links per animal mutualist.

Robustness measures the robustness of the system to extinctions, calculated as the area under the secondary extinction curve. Robustness 1 reflects a gentle extinction curve, a very robust system. 0 reflects a fragile system with abrupt extinctions as species go extinct (Memmott et al., 2004).

At species level

Species strength measures the sum of dependencies of the animals on a plant, or the plants on an animal (*see also* Bascompte et al., 2006).

PDI, Paired difference index depicts a species' **resource range**. A species having PDI zero is a perfect generalist, while a species having PDI one is a perfect specialist. PDI is measured as: measured as:

$$PDI = \frac{\mathrm{sum}(P_1\ -\ P_i)}{(\mathrm{H} - 1)}$$

Where P_1 is the highest number of interactions in a link, while P_i are the values that remain, and H is the number of potential partners of a node.

Proportional similarity represents specialization through dissimilarity between resource use and availability (estimated from high weight/low weight) as proposed by Feinsinger et al. (1981).

Betweenness describes the centrality of a species by its position relevant to other nodes in the network. It measures the dependencies of other nodes of a given node by the number of times it acts as the shortest path between other nodes. High betweenness thus indicates a node's control of the network. Weighted betweenness is betweenness represented with weights.

Closeness describes the centrality of a node by its path lengths to other nodes, in which high closeness reflects a node's ability to provide access efficiency for other nodes. It is the inverse of the average distance from the focal nodes to other nodes. In this study, closeness is weighted.

Connectors and **hubs** in the network are recognized with c and z values of at least 0.62 and 2.5 respectively (Guimerà & Amaral, 2005; Olesen et al., 2007). c describes connectivity amongst modules, while z indicates a highly linked node within the module.

Principal Component Analysis (PCA)

I carried out a PCA analysis to understand which ecological factors were driving the seed dispersal network patterns (Hammer et al., 2001). I used network modules as the grouping variable, and four factors – the largest seed dispersed, species strength, weighted closeness, and PDI, as the explanatory variables. All variables were normalised using division by their standard deviations. These four factors were selected and reduced from ten variables that were correlated. The ten variables included the largest seed dispersed, mean size of seed dispersed, the bodyweight of animals, species strength, degree (no. of interactions), weighted-closeness, weighted betweenness, z-values, c-values and PDI of different animals. I found that 1) the largest seed dispersed was correlated with mean seed dispersed and body weight. 2) Species strength was correlated with degree and z values. 3) weighted closeness, weight betweenness, and c values were correlated. 4) PDI was in its own dimension. Hence, only four variables were selected for the final PCA analysis.

Defaunation and Functional Extinction

The roles of generalised dispersers are highly important to the network. Matching the results to the vulnerability status of the dispersers (refer Table 4.02), several highly connected species are currently vulnerable (IUCN red list, Table 4.02). I compared the outcome of defaunation through simulations of extinction (R package bipartite, Dormann, 2014) that involved extinction of the most to least connected species (Dunne et al., 2002b; Memmott et al., 2004), the random loss of species (Dunne et al., 2002b; Memmott et al., 2004), and the loss of the most specialised species (e.g. Vázquez & Aizen, 2003; Memmott et al., 2004) as they appear to be at risk of extinction (Rathcke & Jules, 1993; Olesen & Jain, 1994). I interpreted extinction as functional extinction rather than the complete loss of species that can be tied with other factors.

RESULTS

Frugivory and Seed Dispersal Interactions

The sampled plant community included 164 plant species and 34 animal taxa, of which animals dispersed 146 plant species. In this chapter, a single species taxon is described by its full common name (e.g. Malayan tapir), and a multi-species taxon is described in the plural form (e.g. macaques). The 18 plant species without an animal disperser were mainly dry fruited wind- or gravity-dispersed species, including *Trigoniastrum hypoleucum*, *Heritiera* sp., *Triomma malaccensis*, *Koompassia malaccensis*, *Koompassia* sp., *Combretum* sp., *Ventilago maderaspatana*, *Gluta wallichii*, *Neesia* sp., *Dipterocarpus* sp., *four Shorea* spp. and four unidentified species (one dry-fruited, three fleshy species). Combining evidence from transects (seeds in faces, teeth marks on fruits and camera traps), measured fruit traits, LEK and observations from published papers, I identified 1919 frugivory and seed handling interactions – of which 1229 (64.1%) are assigned as seeds dispersed, 687 (35.8%) as seeds undispersed (e.g. predated; Table 4.10).

The mean number of plant species consumed by the community was 52±30 (mean±SD), and the mean number of species dispersed by the community was 36±20. By the total number of interactions (degree), important frugivores that were also important dispersers are gibbons, the Asian elephant, rats, binturong, macaques, hornbills, civets, and flying fox. Animals less dominant in frugivory but were important seed dispersers were Asian fairy-bluebird, barbet, the Malayan sun bear, bats, and Sambar deer. Animals that appeared more reliant on other animals for dispersal were langurs, wild boar, and porcupines. Most frugivores were of relatively poor to intermediate importance in their seed dispersal service (Fig. 4.04).

Table 4.10 Frequency of seed treatment and published records (references) associated with a seed treatment. Abbreviations: No. = number. Int. = interactions.

Seed treatment (Dispersed seeds)	**No. of interactions**	**% total dispersed, n=1229**	**% total consumed, N=1919**	**References (refs.) matching seed dispersal int. of plant genera**
Seeds swallowed and defecated	714	58.3	37.4	336 frugivory refs., 144 confirmed seeds swallowing.
Fruits carried and seeds spat by birds	200	16.3	10.4	49 frugivory refs., 20 confirmed seeds dropped.
Mouth carrying of fruits by bats, including the Malayan flying fox	84	6.8	4.4	65 frugivory refs., 9 confirmed mouth-carrying.
Carried by human	26	2.1	1.4	None
Fruits spat by macaques	47	3.8	2.4	35 frugivory refs., 17 seeds confirmed seeds spat.
Seeds regurgitated by ruminants	49	4.0	2.6	15 frugivory refs., 2 confirmed seeds regurgitated.
Seeds hoarded by rodents	106	8.6	5.5	36 frugivory refs., 18 confirmed seeds hoarded.
Total dispersed	***1229***		**64.0%**	
Seed treatment (Undispersed seeds)		**% total undispersed, n=687**	**% total consumed, N=1919**	
Seed destroyed or predated	417	60.7	21.7	167 frugivory refs., 86 confirmed seeds predated or destroyed.
Seeds dropped near the parent plant	270	39.3	14.1	63 frugivory refs., 4 confirmed seeds dropped.
Undispersed	**687**		**35.8%**	
Total consumed	**1919 (3 unknown seed treatments)**			

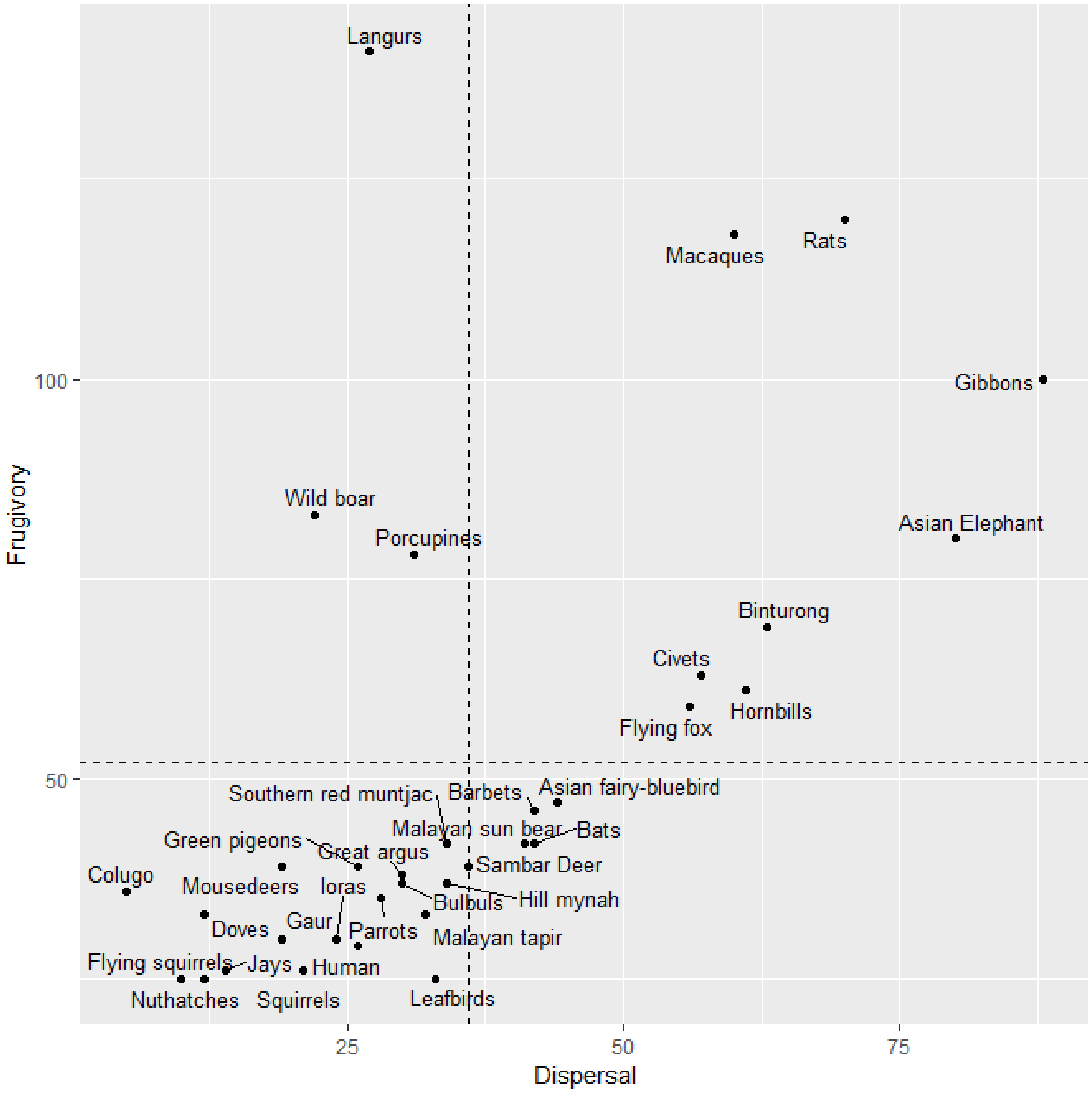


Figure 4.04 Dispersal-Frugivory degree by different animals. The dotted line represents the mean degree of frugivory (52±30) and dispersal (36±20) of the community of animals.

Table 4.11 Frugivory and seed dispersal interactions of birds and the frequency of different seed treatments contributed by the taxa.

Birds	**No. of species swallowed & defecated**[1]	**Seeds carried & spat**	**Seeds carried & spat limit assigned**[2]	**Seeds destroyed**[3]	**Seeds dropped**[4]	**Sum consumed**	**% network frugivory** (consumed/ 1919*100%)	**Sum Dispersed**	**% consumed dispersed** (dispersed/consumed*100%)	**% network dispersal** (dispersed/ 1229*100%)
Asian fairy-bluebird	22	22	20.4 mm	1	2	**47**	2.4	**44**	**93.6**	3.6
Barbets	18	24	19.9 mm	1	3	**46**	2.4	**42**	**91.3**	3.4
Bulbuls	15	15	13.2 mm	0	7	**37**	1.9	**30**	**81.1**	2.4
Doves	6	6	10.8 mm	6	15	**33**	1.7	**12**	**36.4**	1.0
Great Argus[2]	14	16	21 mm	1	7	**38**	2.0	**30**	**78.9**	2.4
Green pigeons[2]	14	12	15 mm	5	8	**39**	2.0	**26**	**66.7**	2.1
Hill Mynah	17	17	19.9 mm	1	2	**37**	1.9	**34**	**91.9**	2.8
Hornbills[7]	23	38	55 mm	0	0	**61**	3.2	**61**	**100.0**	5.0
Ioras	14	10	11.4 mm	0	6	**30**	1.6	**24**	**80.0**	2.0
Jays	9	5	10.8 mm	0	12	**26**	1.4	**14**	**53.8**	1.1
Leafbirds	16	17	15 mm	0	2	**35**	1.8	**33**	**94.3**	2.7
Nuthatches	7	5	10.8 mm	2	11	**25**	1.3	**12**	**48.0**	1.0
Parrots	15	13	15 mm	5	2	**35**	1.8	**28**	**80.0**	2.3
Sum	**190**	**200**		**22**	**77**	**489**	25.5	**390**		31.7
Mean ±SD	**15±5**	**15±9**		**2±2**	**5±5**	**38±10**	**2±1**	**30±14**	76.6±19.8	**2±1**

[1] **Defecated seeds** – Upper limit of seeds defecated by hornbills were set at **5.4mm**, other birds at 5mm according to the following references: barbets with wide gape defecate seed with length around 4.9mm ±0.8 mm (Leighton, 1982); hornbills defecate seeds with seed diameter up to 5.4mm (Kitamura et al., 2008a).

[2] **Regurgitation limit** – Lower limit followed defecated seeds refs.; upper limits follow fruit width of the largest 'indehiscent drupe-fruit' or 'largest dehiscent-fruit seed' swallowed, as indicated by at least two local informant groups. The upper limit represents the bill limit of a bird. Fruits within this size limit are deemed to have higher chances of being carried away, rather than dropped by birds directly under the parent plant.
Indehiscent fruit criteria: seed width > lower limit, fruit width ≤ upper limit; **dehiscent fruit criteria:** lower limit > seed width ≤ upper limit.
Hornbills regurgitation upper limit followed 55mm (Corlett, 2017).
Great Argus regurgitation upper limit followed 21mm Davison (1981).
Green pigeon's regurgitation limit – close to ref. *Treron australis* ca 13mm, Dowsett-Lemaire (1988).

[3] **Seed predation** – Local knowledge of frugivory acknowledgment from ≥2 groups, and at least one indicated as seed predation / destroyed or having supporting ref from an identical genus.

[4] **Seeds dropped – Indehiscent fruit criteria:** fruit width > upper limit; **Dehiscent fruit criteria:** seed width > upper limit

Table 4.12 Frugivory and seed dispersal interactions of arboreal mammals excluding rodents, and the frequency of different seed treatment contributed by the taxa.

Taxa	**No. of species swallowed & defecated**	**Defecated seed limit assigned**[1]	**Seeds carried & spat**[2]	**Seed predated/ destroyed**[3]	**Seeds dropped**[4]	**Unidentified seed treatment**	**Sum consumed**	**% network frugivory** (consumed/ 1919*100%)	**Sum Dispersed**	**% consumed dispersed** (dispersed/consumed*100%)	**% network dispersal** (dispersed/ 1229*100%)
Bats	7	0.8 mm	35	0	0	0	**42**	2.2	**42**	100.0	3.4
Malayan flying fox[1]	7	4mm	49	2	1	0	**59**	3.1	**56**	94.9	4.6
Gibbons[1]	88	24.5mm	0	2	10	0	**100**	5.2	**88**	88.0	7.2
Macaques	13	4.5 mm	47	43	14	1	**118**	6.1	**60**	50.8	4.9
Langurs	27	10.8 mm	0	74	40	0	**141**	7.3	**27**	19.1	2.2
Binturong[1]	63	20.3 mm	0	0	6	0	**69**	3.6	**63**	91.3	5.1
Civets	57	20.3 mm	0	0	6	0	**63**	3.3	**57**	90.5	4.6
Colugo	5	1.2 mm	0	0	31	0	**36**	1.9	**5**	13.9	0.4
Malayan sun bear[1]	41	28.2 mm	0	0	1	0	**42**	2.2	**41**	97.6	3.3
Sum	**308**		**131**	**121**	**109**	**1**	**670**	34.9	**439**		35.7
Mean ±SD	34±30		15±23	13±27	12±14	0.1±0.3	74±37	4±2	49±24	71.8±34.6	4±2

[1] **Defecated seed limit** – Upper limits (swallowing limits) followed the seed width of the largest seed swallowed as indicated by at least two local informant groups.
Malayan flying fox swallowed seeds limit followed Richards, 1990.
Gibbons seed swallowed limit followed 24.5mm (Dai et al., 2018); data indicated 19.2mm
Binturong and civets seed swallowed limit followed 20.3mm (Nakashima et al., 2010), except for *Monocarpia marginalis* and *Willughbeia cf. flavescens* due to fruit structure.

[2] **Seeds carried by bats** – Upper limit for average-sized fruit bats, 200g (van der Pijl, 1982); upper limit Malayan flying fox, 500g (Bollen et al., 2004).
Seeds spat by macaques – as indicated by at least two local informant groups or one ref. supporting 'seed spat' as seed treatment of plant genus. Unless fruits are relatively large (>30mm), 'seeds dropped' are switched to 'seeds spat'.

[3] **Seeds destroyed** – Local knowledge of frugivory acknowledgment from ≥2 groups, and at least one indicated as seed predation / destroyed or having supporting ref from an identical genus.

[4] **Seeds dropped** – Seed width > swallowing limit.

Table 4.13 Frugivory and seed dispersal interactions of terrestrial mammals excluding rodents, and the frequency of different seed treatment contributed by the taxa.

Taxa	**No. of species swallowed & defecate**	**Defecated seed limit assigned**[1]	**Seeds carried/ regurgi-tated**[2]	**Seeds destroyed**[2]	**Seeds dropped**[3]	**Unidentified seed treatment**	**Sum consumed**	**% network frugivory** (consumed/ 1919*100%)	**Sum Dispersed**	**% consumed dispersed** (dispersed/consumed*100%)	**% network dispersal** (dispersed/ 1229*100%)
Asian Elephant	80	46.9 mm	0	0	0	0	**80**	4.2	**80**	100.0	6.5
Gaur	17	10.6 mm	2	10	1	0	**30**	1.6	**19**	63.3	1.5
Mousedeers[2]	5	1.1 mm	14	1	19	0	**39**	2.0	**19**	48.7	1.5
Southern red Muntjac	17	8.2 mm	17	2	5	1	**42**	2.2	**34**	81.0	2.8
Sambar deer	20	8.2 mm	16	2	1	0	**39**	2.0	**36**	92.3	2.9
Malayan Tapir	32	25.7 mm	0	0	1	0	**33**	1.7	**32**	97.0	2.6
Wild boar	22	28 mm	0	61	0	0	**83**	4.3	**22**	26.5	1.8
Human	0	NA	26	3	0	0	**29**	1.5	**26**	89.7	2.1
Sum	**193**		**75**	**79**	**27**	**1**	**375**	19.5	**268**		21.8
Mean ±SD	24±25		9±10	10±21	3±7	0.1±0.4	47±22	2±1	34±20	75±26	3±2

[1] **Defecated seed limit** – Upper limits (swallowing limits) followed the seed width of the largest seed swallowed as indicated by at least two local informant groups. **Malayan tapir seed swallowed limit** close to Sridhara et al., 2016 (seed width 26mm).

[2] **Seeds carried /regurgitated /destroyed /hoarded /destroyed (including fragmented seeds)** — Local knowledge of frugivory acknowledgment from ≥2 groups, and at least one indicated as seeds carried /regurgitated /predated /hoarded/ destroyed or having supporting ref from an identical genus.

Regurgitation limit:
gaur: 28.2mm (LEK)
mousedeer set as seed width 17mm (Sridhara et al., 2016).
Southern red muntjac and sambar deer followed LEK (28.2mm) although stated as 80mm in Sridhara et al. (2016)

[3] **Seeds dropped** – Seed width > swallowing limit.

Table 4.14 Frugivory and seed dispersal interactions of rodents, and the frequency of different seed treatment contributed by the taxa.

Taxa	**No. of species swallowed & defecated**	**Defecated seed limit assigned**[1]	**Hoarding**[2]	**Seeds destroyed**[2]	**Seeds dropped**[3]	**Unidentified seed treatment**	**Sum consumed**	**% network frugivory** (consumed/ 1919*100%)	**Sum Dispersed**	**% consumed dispersed** (dispersed/consumed*100%)	**% network dispersal** (dispersed/ 1229*100%)
Flying squirrels	5	1.1 mm	5	2	25	0	**37**	1.9	**10**	27.0	0.8
Squirrels	6	1.1 mm	15	107	26	0	**154**	8.0	**21**	13.6	1.7
Porcupines	9	5.4 mm	22	45	1	1	**78**	4.1	**31**	39.7	2.5
Rats	6	Unclear[1]	64	45	5	0	**120**	6.3	**70**	58.3	5.7
Sum	**26**		**106**	**199**	**57**	**1**	**389**	20.3	**132**		10.7
Mean ±SD	7±2		27±26	50±43	14±13	0.3±0.5	97±51	5±3	33±26	35±19	3±2

[1] **Defecated seed limit** – Upper limits (swallowing limits) followed the seed width of the largest seed swallowed as indicated by at least two local informant groups. Rats have no plant species indicated as defecated; seeds may be partly damaged or dropped.

[2] **Seeds carried /regurgitated /destroyed /hoarded /destroyed (including fragmented seeds)** — Local knowledge of frugivory acknowledgment from ≥2 groups, and at least one indicated as seeds carried /regurgitated /predated /hoarded /destroyed or having supporting ref from an identical genus.

[3] **Seeds dropped** – Seed width > swallowing limit.

The median fruit size of plant species in the community is 19mm (mean 27±22mm) and the median seed size is 9mm (mean 11±8mm) (Appendix Table A4.1). The mean diameter (mm) of seeds dispersed by the community through swallowing is 7±6 (min.=1, max.=47), spat by macaques is 11±4 (min.=5, max.= 25), regurgitated by ruminants is 15±6 (min.=4, max.=28), hoarded is 16±9 (min.=4, max.=47), and carried by birds, bats and human is 10±6 (min.=1, max=47) (Fig. 4.05; Table 4.15).

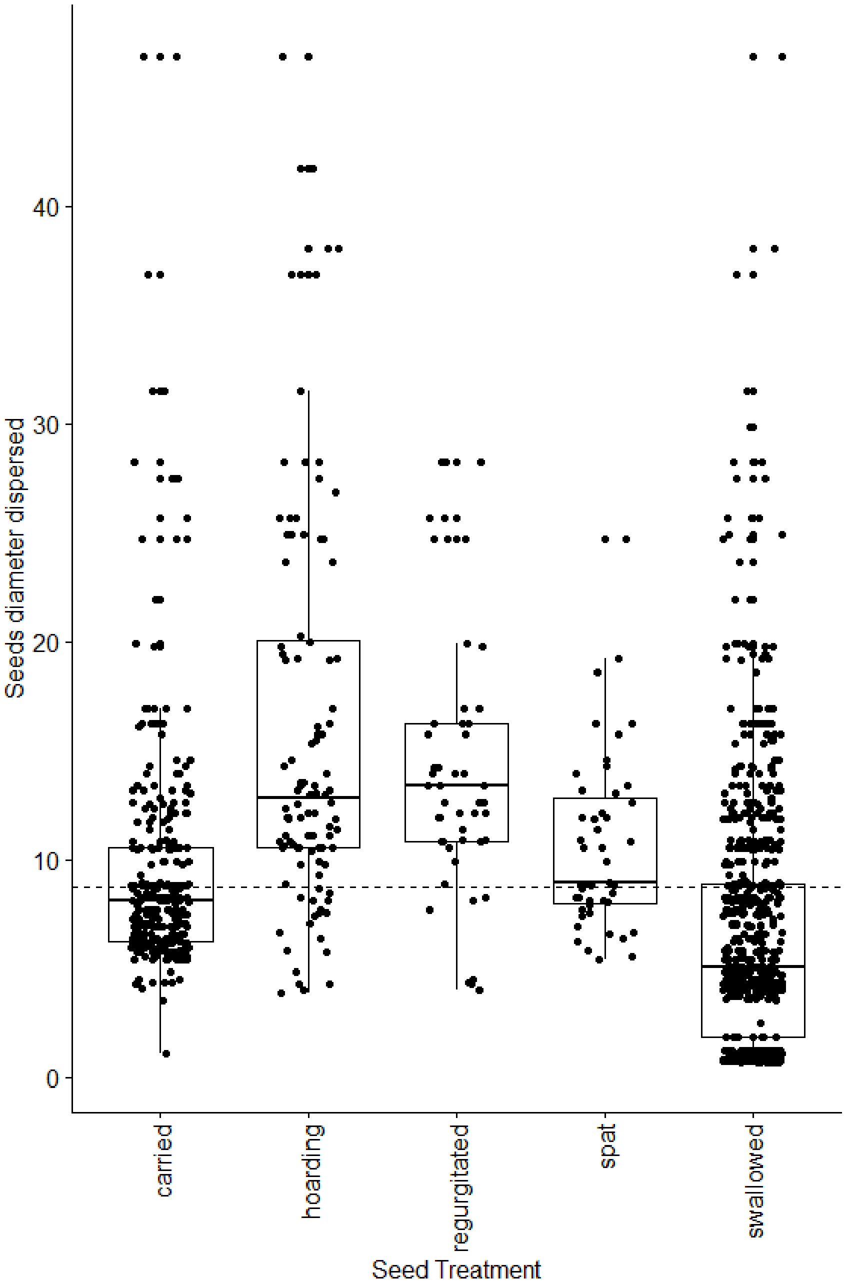


Figure 4.05 Boxplots of seeds sizes dispersed through different seed treatment methods. The dotted line is the mean of seeds dispersed (9mm, N=1219).

Table 4.15 Seed sizes dispersed through different seed treatments

Dispersal	N	median	mean	sd	min	max
carried	307	8	10	6	1	47
hoarding	104	13	16	9	4	47
regurgitated	49	13	15	6	4	28
spat	47	9	11	4	5	25
swallowed	712	5	7	6	1	47

The weights of links are important to defining network structures. By number of interactions (N=1919), frugivory were mainly represented by squirrels (154, 8%), langurs (141, 7.3%), rats (120, 6.1%), macaques (118, 6.1%), gibbons (100, 5.2%), wild boar (83, 4.3%) and the Asian elephant (80,4.2%) (Table 4.11 to 4.14). Taking weights into consideration, the dominant frugivores were squirrels, langurs, macaques, rats, gibbons, wild boar, and binturong (Fig. 4.06). Seed dispersal interactions (n=1229) were mainly represented by gibbons (88, 7.2%), the Asian elephant (80, 6.5%), rats (70, 5.7%), binturongs (63, 5.1%), hornbills (61, 5.0%), macaques (60, 4.9%), civets (57, 4.6%) and the Malayan flying fox (56, 4.6%) (Table 4.11 to 4.14). Weighted seed-dispersal interactions were represented largely by gibbons, binturong, civets, the Asian elephant, Malayan sun bear, and macaques (Fig. 4.07).

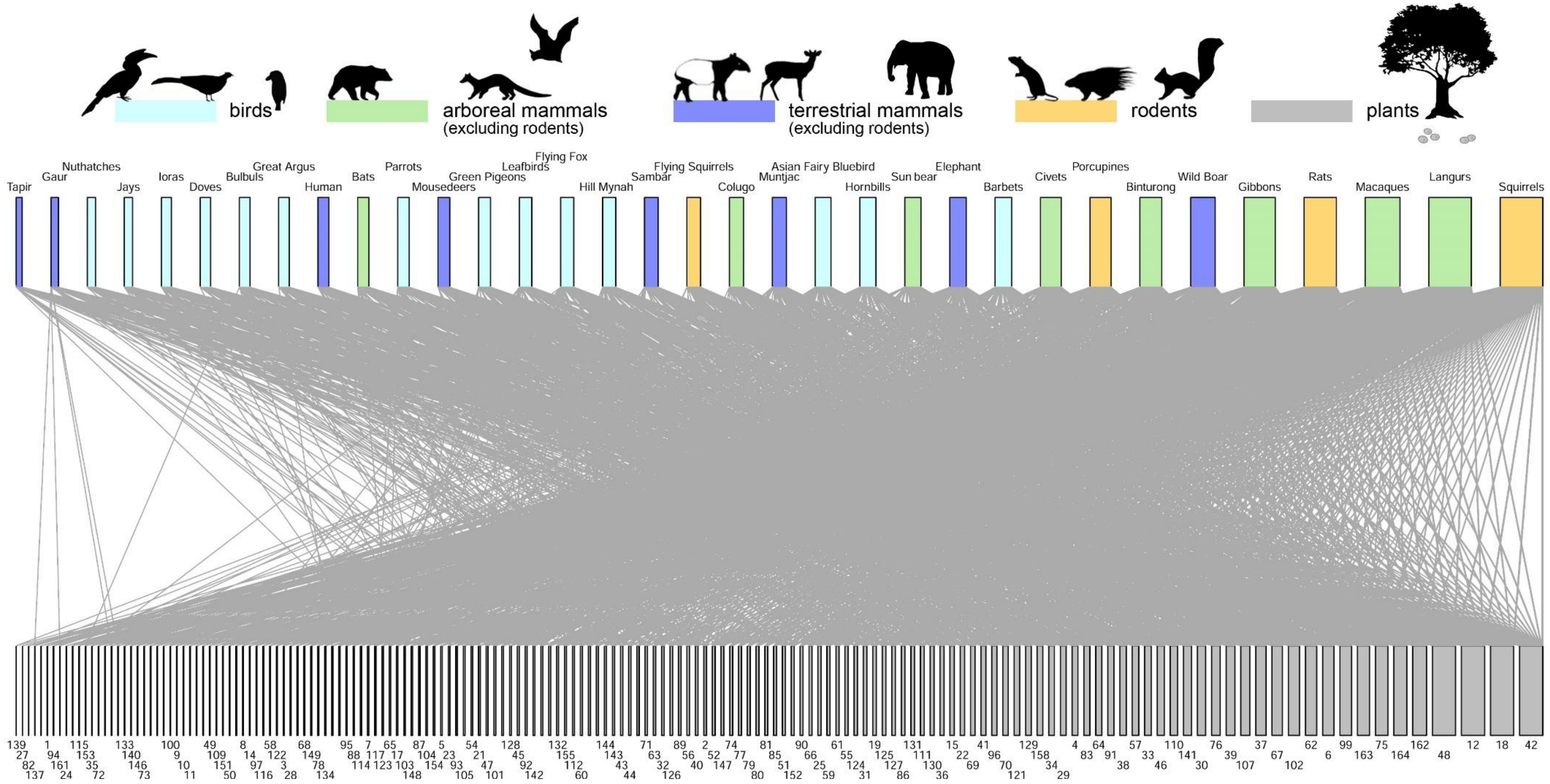


Figure 4.06 Bipartite graph of a weighted plant-animal frugivory network involving 164 plants (lower level) and 34 frugivores (upper level) in RBSP, Malaysia; arranged from the least linked (left) to the highest linked (right) taxa. The thickness of the lines indicates the weights of the interactions. Weights represent the frequency of observations (see Methods, Interaction Matrix: Weighted network). A list of plants and their respective codes can be found in Appendix Table A4.1.

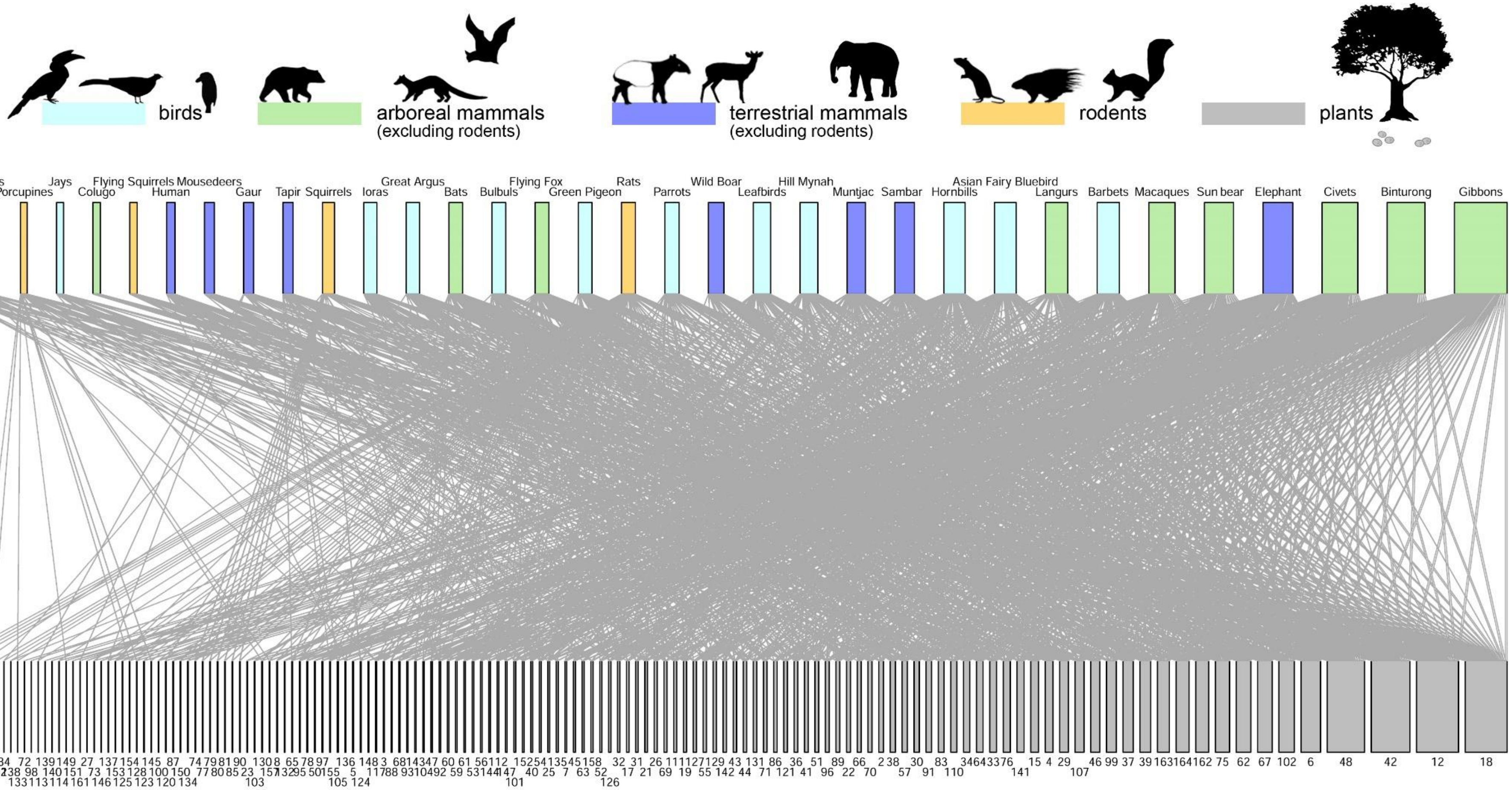


Figure 4.07 Bipartite graph of weighted plant-animal seed dispersal network involving 164 plants (lower level) and 34 frugivores (upper level) in RBSP, Malaysia; arranged from the least linked and weighted (left) to the highest linked and weighted (right) taxa. The thickness of the lines indicates the weights of the interactions. Weights represent seed dispersal effectiveness, i.e. frequency of observations x modes of dispersal grouped by seed-handling (see Methods, Interaction Matrix: Weighted network). A list of plants and their respective codes can be found in Appendix Table A4.1.

The Seed Dispersal Network of Belum

Network Properties

I found the Belum seed dispersal network to be nested, connected, and generalised. Comparing the Belum seed dispersal network with the Patefield null model, results were significantly more nested (weighted NODF 26.3, $p < 0.001$) and connected (weighted connectance 0.142, $p<0.001$) (Table 4.15; Appendix Fig. A4.18), with similar interaction evenness 0.796, lower complementary specialization, H_2' (0.225, $p<0.001$) but higher linkage density (i.e., average vulnerability and generality 25.6) than expected. See Appendix Table A4.2 for comparison with existing networks.

Table 4.16 Network metrics of the seed dispersal network comparing to 1000 networks using the Patefield null model. CI = confidence intervals.

Metric	Estimate	Null model (N=1000)	
		Mean	Upper and lower CI
Weighted connectance (C)	0.142	0.0928	0.0914 – 0.0947
Weighted NODF	26.3	11.6	10.6 – 12.7
Specialization (H_2')	0.225	0.468	0.458 – 0.478
Linkage density	25.6	16.7	16.4 – 17.1
Interaction evenness	0.796	0.796	0.796 –0.796

Community Properties

The animal community reflected a high mean number of shared partners (14), generality (34.5) – i.e. the effective mean number of links per animal mutualists, and robustness to random extinction (0.82). Plants had a low mean number of shared partners (3), vulnerability (16.8) – i.e., the effective mean number of links per plant mutualists, and robustness (0.96).

The Belum Seed Dispersal Network Structure

The bipartite network consisted of four modules (likelihood= 0.289, i.e., modularity) (Fig. 4.08; Appendix Fig. A4.18). In 50 runs, 56% of runs reflected a computation of four modules, 34% five modules, 8% three modules, and 2% six modules. I thus present the network with four modules. Amongst the simulations with four modules detected, langurs (56%) were more often assigned individually in a single module. Other combinations were langur-gaur, langur-gibbon, langur-porcupine, porcupine, and porcupine-Southern red muntjac. Most other species were assigned to the same module combinations. The first module comprised twelve bird groups (ioras, parrots, leafbirds, bulbuls, jays, nuthatches, the Asian fairy-bluebird, the Hill mynah, barbets, green pigeons, doves, and hornbills) and 34 plant species. Langur and eight plant species solely represented the second module. The third module included eleven mammals (Southern red muntjac, the sambar deer, Malayan flying fox, macaques, gibbons, human, civets, binturong, the Malayan sun bear, Malayan tapir, and Asian elephant) and 74 plant species. This module accounted for the majority (49.5% of 1229) of the seed dispersal interactions. Most large-bodied species were assigned under this module (Table 4.17). The fourth comprised nine animal taxa (the Great argus, rats, squirrels, flying squirrels, porcupine, wild boar, mousedeers, gaur, colugo, and bats) and 30 plant species in the seed dispersal network.

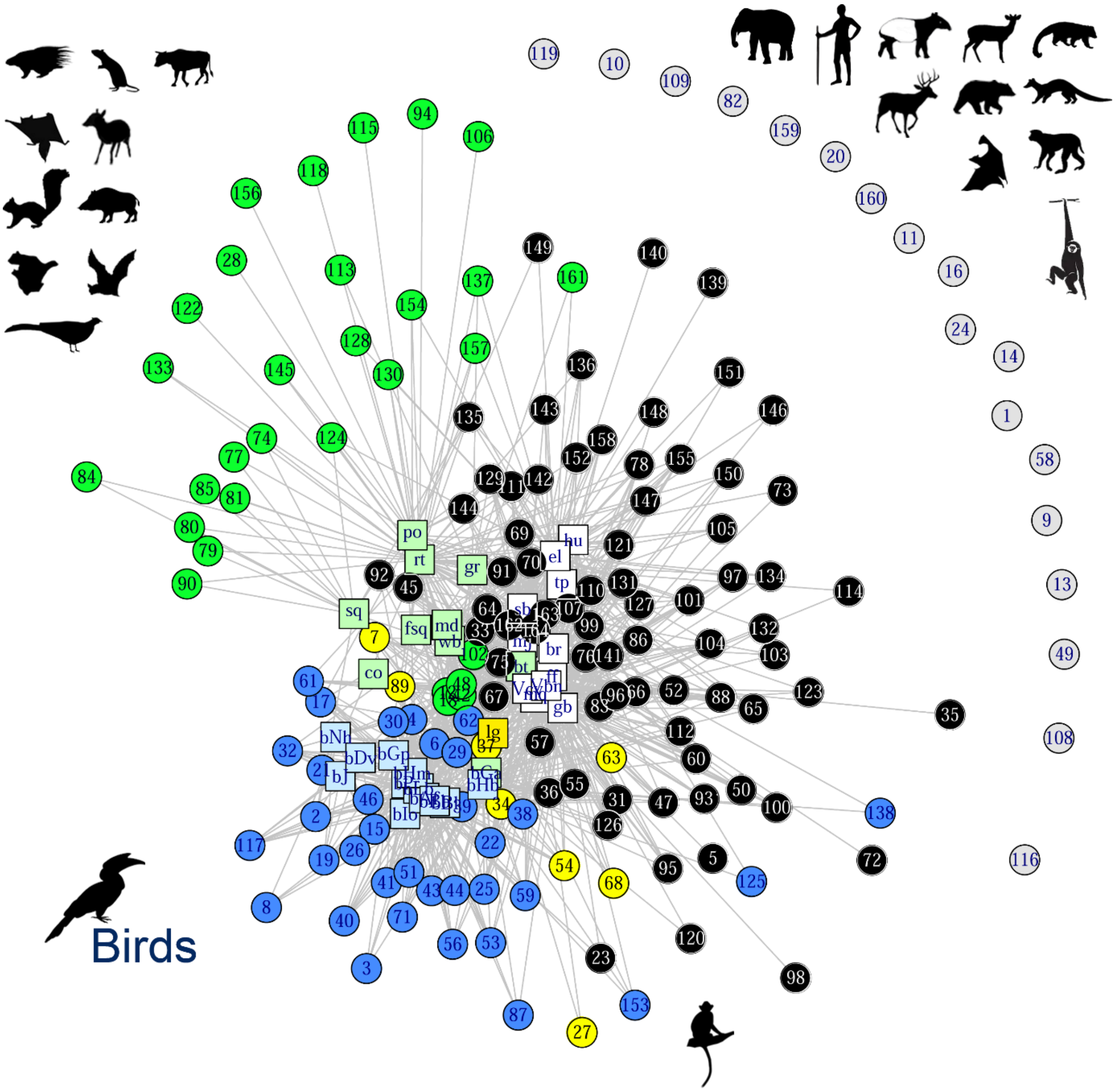


Figure 4.08 The seed dispersal network of the Belum rainforest, Malaysia. (Left) Modules are represented by different colours: module 1 (green), module 2 (blue), module 3 (black and white), and module 4 (yellow). Plants with no animal dispersers are unconnected (grey). Circles represent plants while squares represent animals: human (hu), Asian elephant (el), Malayan tapir (tp), Malayan sun bear (br), sambar deer (sb), gaur (gr), Southern red muntjac (mj), binturong (bt), Malayan flying fox (ff), macaques (mq), gibbons (gb), binturong (Vbn), civets (Vcv), langurs (lg), porcupine (po), rats (rt), flying squirrels (fsq), wild boar (wb), mousedeer (md), squirrels (sq), colugo (co), Great argus (bGa), hornbills (bHb), Asian fairy-bluebird (bAf), ioras (bIo), parrots (bPr), leafbirds (bLb), bulbuls (bBl), jays (bJ), the Hill mynah (bHm), barbets (bBb), and doves (bDv).

Table 4.17: Body weights of animals in the community. In bold: important seed dispersers according to Figure 4.05.

Animal	**Module**	**Group**	**Order**	**Family**	**Body Weight (kg)**
Asian Elephant	3	tr. mam	Proboscidea	Elephantidae	4200
Gaur	4	tr. mam	Artiodactyla	Bovidae	720
Malayan Tapir	3	tr. mam	Perissodactyla	Tapiridae	395
Sambar deer	3	tr. mam	Artiodactyla	Cervidae	323
Wild boar	4	tr. mam	Artiodactyla	Suidae	87.5
Human	3	tr. mam	Primates	Hominidae	75
Malayan sun bear	3	tr. mam	Canivora	Ursidae	53.5
Binturong	3	ar. mam	Canivora	Viverridae	21.5
Southern red muntjac	3	tr. mam	Artiodactyla	Cervidae	18
Porcupines	4	rodents	Rodentia	Hystricidae	8
Langurs	2	ar. mam	Primates	Cercopithecidae	7
Gibbons	3	ar. mam	Primates	Hylobatidae	5.9
Mousedeers	4	tr. mam	Artiodactyla	Tragulidae	5.3
Civets	3	ar. mam	Canivora	Viverridae	3.5
Hornbills	1	birds	Bucerotiformes	Bucerotidae	2.8
Great Argus	1	birds	Galliformes	Phasianidae	2
Macaques	3	ar. mam	Primates	Cercopithecidae	2
Colugo	4	ar. mam	Dermoptera	Cynocephalidae	1.5
Malayan flying fox	3	ar. mam	Chiroptera	Pteropodidae	1.1
Flying squirrels	4	rodents	Rodentia	Sciuridae	0.7
Bats	4	ar. mam	Chiroptera	Pteropodidae	0.55
Jays	1	birds	Passeriformes	Corvidae	0.24
Hill Mynah	1	birds	Passeriformes	Sturnidae	0.22
Green pigeons	1	birds	Galliformes	Columbidae	0.21
Squirrels	4	rodents	Rodentia	Sciurinae	0.2
Parrots	1	birds	Psittaciformes	Psittaculidae	0.18
Doves	1	birds	Columbiformes	Columbiformes	0.16
Rats	4	rodents	Rodentia	Muridae	0.1
Asian fairy-bluebird	1	birds	Passeriformes	Irenidae	0.075
Bulbuls	1	birds	Passeriformes	Pycnonotidae	0.074
Barbets	1	birds	Piciformes	Megalaimidae	0.041
Leafbirds	1	birds	Passeriformes	Chloropseidae	0.03
Nuthatches	1	birds	Passeriformes	Sittidae	0.015
Ioras	1	birds	Passeriformes	Aegithinidae	0.014

In this network, I found 18 plant species without an animal disperser. 14 were mainly non-zoochoric, dry fruited wind- or gravity-dispersed species, including *Trigoniastrum hypoleucum* from the Trigoneaceae family, *Heritiera* sp. (Sterculiaceae), *Triomma malaccensis* (Burseraceae), *Koompassia malaccensis* (Fabaceae), *Koompassia* sp. (Fabaceae), *Combretum* sp. (Combretaceae), *Ventilago maderaspatana* (Rhamnaceae), *Gluta wallichii* (fam. Anacardiaceae), *Dipterocarpus* sp. (fam. Dipterocarpaceae), *four Shorea* spp. (Dipterocarpaceae) and an unidentified sp. (Cengang*). *Neesia* sp. (Malvaceae) is a dehiscent fruit consumed by Orangutans, and possibly by hornbills that regurgitate the seeds after swallowing the arils (cited in Schaik & Knott, 2001). Between the three unidentified fleshy species, one is a multi and large-seeded (Simelyong*; seed diameter 26.4mm) fruit. Its seeds were found together at the same spot, cleaned, and without any pulp attached to it. With latex on its seed, it shared similar characteristics as *Willughbeia cf. flavescens* (Apocynaceae). Another two fleshy species — Nyapang* and Rangoid* (a V-shaped fruit) were small fruits.

Degree Distribution

Degree for animals in the matrix followed a truncated power-law distribution, $\Pr(>|t|) < 0.001$, $R^2=0.995$, as in most seed dispersal networks (Bascompte & Jordano, 2014). The probability distribution for plants was less clear – either following an exponential $\Pr(>|t|) < 0.001$, $R^2=0.997$, AIC (-118.0) distribution, or a truncated power-law distribution $\Pr(>|t|) = 0.1$, $R^2=0.997$, AIC (-119.2) (Appendix Fig. A4.19).

Species Properties and Functionally Important Species

The properties of all 34 animal taxa/species are summarised in Table 4.18.

***Specialism of animals* —** In the Belum network, I found all animals were specialists with PDI ranging from 0.80 to 0.98 (PDI 0 = perfect generalist, PDI 1 = perfect specialists), although many were highly linked. These animals were generalists from the perspective of the broad ranges of fruit species they consumed (number of links), but the very large diversity of fruit species available meant that they were only dispersing a fraction of these species. I also found PDI (R=-0.83, df=32, p< 0.001) correlates negatively with species' degree (Appendix Fig. A4.20), and the differences between PDI values were small (mean 0.92±0.04) (Table 4.18). To avoid confusion, I thus described highly connected animals as generalised animals, and less connected animals as specialised animals. I compared them in terms of generalism.

In the Belum seed dispersal network, the average number of plants that an animal taxon dispersed was high (degree: 36±20). Highly connected animals include gibbons (degree: 88), the Asian elephant (80), rats (70), binturong (63), hornbills (61), macaques (60), civets (57) and the

Malayan flying fox (56) (Fig. 4.09; Table 4.18). From individual modules, hornbills, the Asian fairy-bluebird, and barbets are important for module one, langurs for module two, gibbons, Asian elephant, binturong, macaques, civets and the Malayan flying fox for module three, and rats and bats for module four (Fig. 4.09).

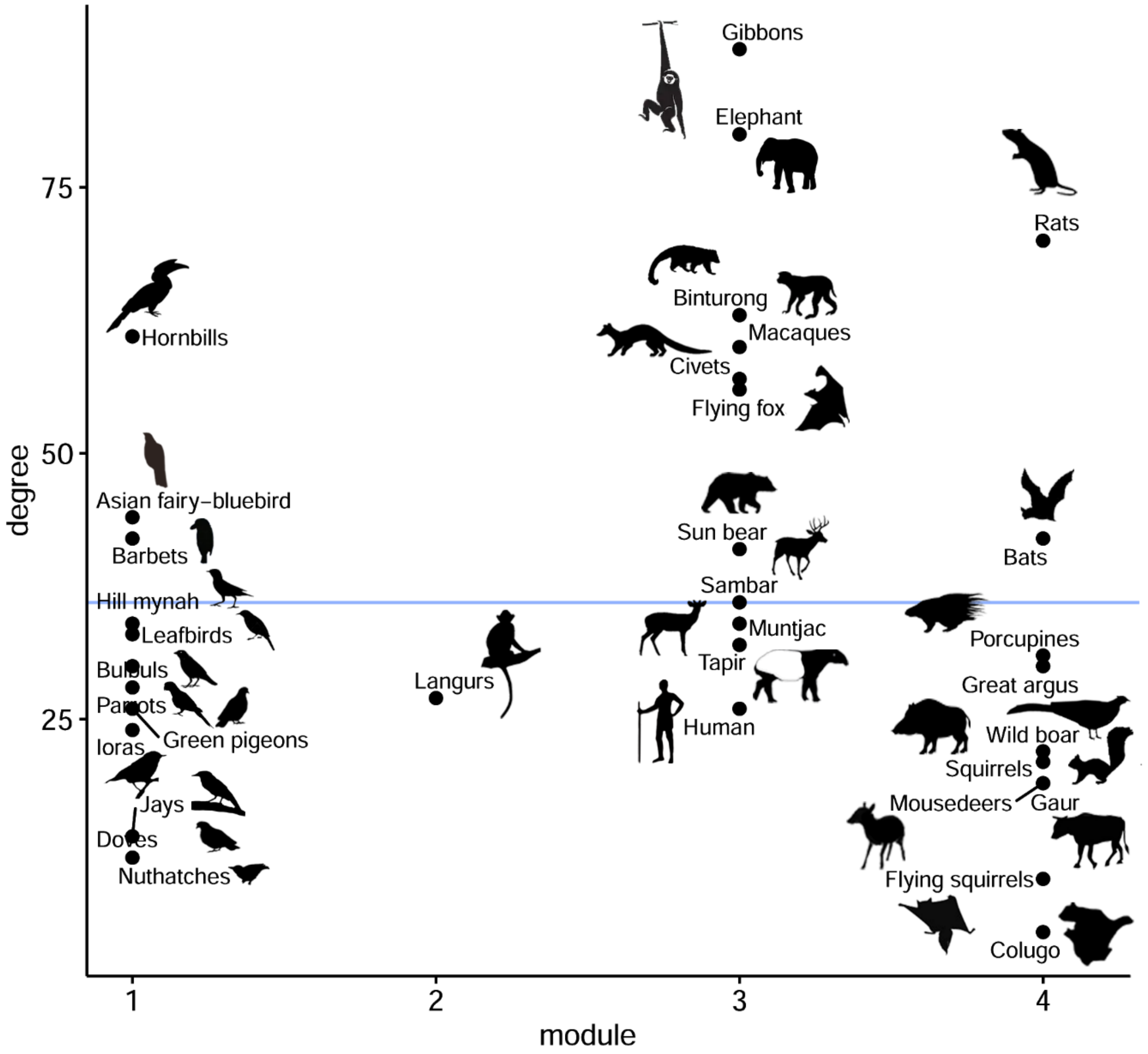


Figure 4.09 Degree and module representation of animals in the Belum seed dispersal network. The blue line represents the average degree of animals (36±20).

Table 4.18 Descriptive summary of species properties indicating seed dispersal influence on plants, module, and the overall network (arranged according to degree number: high to low); in green (top 3), in yellow (top 10).

Mod	**Group**	**Animal**	**Family**	**Body Wt.**	**Largest seed dispersed**	**Deg.**	**PDI**	**Species strength**	**Z**	**C**	**Weighted closeness**	**Weighted betweenness**
				(kg)	(mm)	links	generalism	effects on plants	within module	connect modules	central to network	short paths – central
3	ar. Mam	Gibbons	Hylobatidae	5.9	22	**88**	**0.80**	**20.0**	**2.2**	0.35	**0.059**	**0.92**
3	tr. Mam	Asian Elephant	Elephantidae	4200	**47**	**80**	**0.87**	**17.2**	**1.56**	0.36	0.032	**0.0050**
4	rodents	Rats	Muridae	0.1	**47**	**70**	0.93	**14.7**	**2.5**	0.34	0.020	0
3	ar. Mam	Binturong	Viverridae	21.5	20	**63**	**0.86**	**8.1**	**0.17**	0.34	**0.050**	0
1	birds	Hornbills	Bucerotidae	2.8	22	**61**	**0.89**	**6.4**	**1.90**	**0.47**	0.032	0
3	ar. Mam	Macaques	Cercopithecidae	2	25	**60**	**0.90**	**6.5**	-0.19	**0.41**	**0.041**	0
3	ar. Mam	Civets	Viverridae	3.5	17	**57**	**0.84**	**6.0**	-0.20	**0.41**	**0.049**	**0.0075**
3	ar. Mam	Malayan flying fox	Pteropodidae	1.1	**32**	**56**	0.92	3.8	-0.51	0.21	0.025	0
1	birds	Asian fairy-bluebird	Irenidae	0.075	13	**44**	**0.89**	4.8	**1.28**	0.36	**0.035**	**0.010**
1	birds	Barbets	Megalaimidae	0.041	12	**42**	**0.88**	4.2	**1.17**	0.29	**0.036**	**0.045**
4	ar. Mam	Bats	Pteropodidae	0.55	**47**	42	0.94	1.9	-0.61	0.32	0.027	0
3	tr. Mam	Malayan sun bear	Ursidae	53.5	**28**	41	**0.89**	**5.8**	-0.11	0.15	**0.043**	**0.0075**
3	tr. mam	Sambar deer	Cervidae	323	11	36	**0.90**	2.8	-0.66	0.13	**0.033**	0
3	tr. mam	Southern red muntjac	Cervidae	18	**28**	34	0.92	2.8	-0.68	0.20	0.032	0
1	birds	Hill Mynah	Sturnidae	0.22	11	34	0.91	2.8	**0.27**	0.29	0.032	0
1	birds	Leafbirds	Chloropseidae	0.03	12	33	0.93	3.0	0.09	**0.38**	**0.032**	**0.0025**
3	tr. mam	Malayan Tapir	Tapiridae	395	**26**	32	0.91	2.3	-0.77	0.13	0.020	0
4	rodents	Porcupines	Hystricidae	8	**42**	31	0.91	**5.4**	**0.62**	0.27	0.012	0

(continued) Table 4.18 Descriptive summary of species properties indicating seed dispersal influence on plants, module, and the overall network (arranged according to degree number: high to low); in green (top 3), in yellow (top 10).

Mod	**Group**	**Animal**	**Family**	**Body Wt.**	**Largest seed dispersed**	**Deg.**	**PDI**	**Species strength**	**Z**	**C**	**Weighted closeness**	**Weighted betweenness**
				(kg)	(mm)	links	Genera-lism	effects on plants	within module	connect modules	central to network	central with short paths
1	birds	Bulbuls	Pycnonotidae	0.074	13	30	0.93	2.1	-0.17	0.29	0.026	0
1	birds	Great Argus	Phasianidae	2	17	30	0.94	1.7	-0.61	**0.60**	0.027	0
1	birds	Parrots	Psittaculidae	0.18	9	28	0.93	2.0	-0.30	0.25	0.028	0
2	ar. mam	Langurs	Cercopithecidae	7	11	27	0.90	3.8	NA	**0.52**	**0.038**	0
3	tr. mam	Human	Hominidae	75	**47**	26	0.93	1.8	-0.84	0.00	0.017	0
1	birds	Green pigeons	Columbidae	0.21	9	26	0.93	1.7	-0.53	0.27	0.027	0
1	birds	Ioras	Aegithinidae	0.014	9	24	0.95	1.9	-0.37	0.20	0.024	0
4	tr. mam	Wild boar	Suidae	87.5	13	22	0.93	1.3	-0.59	**0.63**	0.031	0
4	rodents	Squirrels	Sciurinae	0.2	**37**	21	0.96	**4.9**	**0.55**	0.09	0.024	0
4	tr. mam	Gaur	Bovidae	720	11	19	0.94	2.7	-0.04	**0.51**	0.020	0
4	tr. mam	Mousedeers	Tragulidae	5.3	16	19	0.96	0.69	-0.59	**0.52**	0.024	0
1	birds	Jays	Corvidae	0.24	8	14	0.97	0.89	-1.03	0.15	0.015	0
1	birds	Doves	Columbiformes	0.16	14	12	0.97	0.79	-1.09	0.28	0.016	0
1	birds	Nuthatches	Sittidae	0.015	8	12	0.97	0.63	-1.22	0.30	0.014	0
4	rodents	Flying squirrels	Sciuridae	0.7	1	10	0.97	0.31	-0.61	**0.49**	0.020	0
4	ar. mam	Colugo	Cynocephalidae	1.5	1	5	0.98	0.20	-0.61	0.22	0.022	0
			Mean±SD	**174±726**	**20±14**	**36±20**	**0.9±0.04**	**4±5**	**0±1.0**	**0.3±0.2**	**0.03±0.1**	**0.03±0.2**

Species strength — Species strength determines the influence of an animal on the plants it dispersed, which in this study defines its strength as a seed disperser. Species strength positively correlates with degree (R=0.88, df=32, p< 0.001) (Appendix Fig. A4.21). The average species strength of an animal in the network was 4.3±4.6. Gibbons (20), the Asian elephant (17.2) and rats (14.7) had exceedingly high species strength, and binturong (8.1), macaques (6.5), hornbills (6.4), civets (6.0), the Malayan sun bear (5.8) and porcupines (5.4) had high species strength (Table 4.18). From individual modules, hornbills, the Asian fairy-bluebird, and barbets in module one, langurs in module two, gibbons and the Asian elephant in module three, and rats in module four had the greatest influence on the dispersal of plants within the modules (Fig. 4.10).

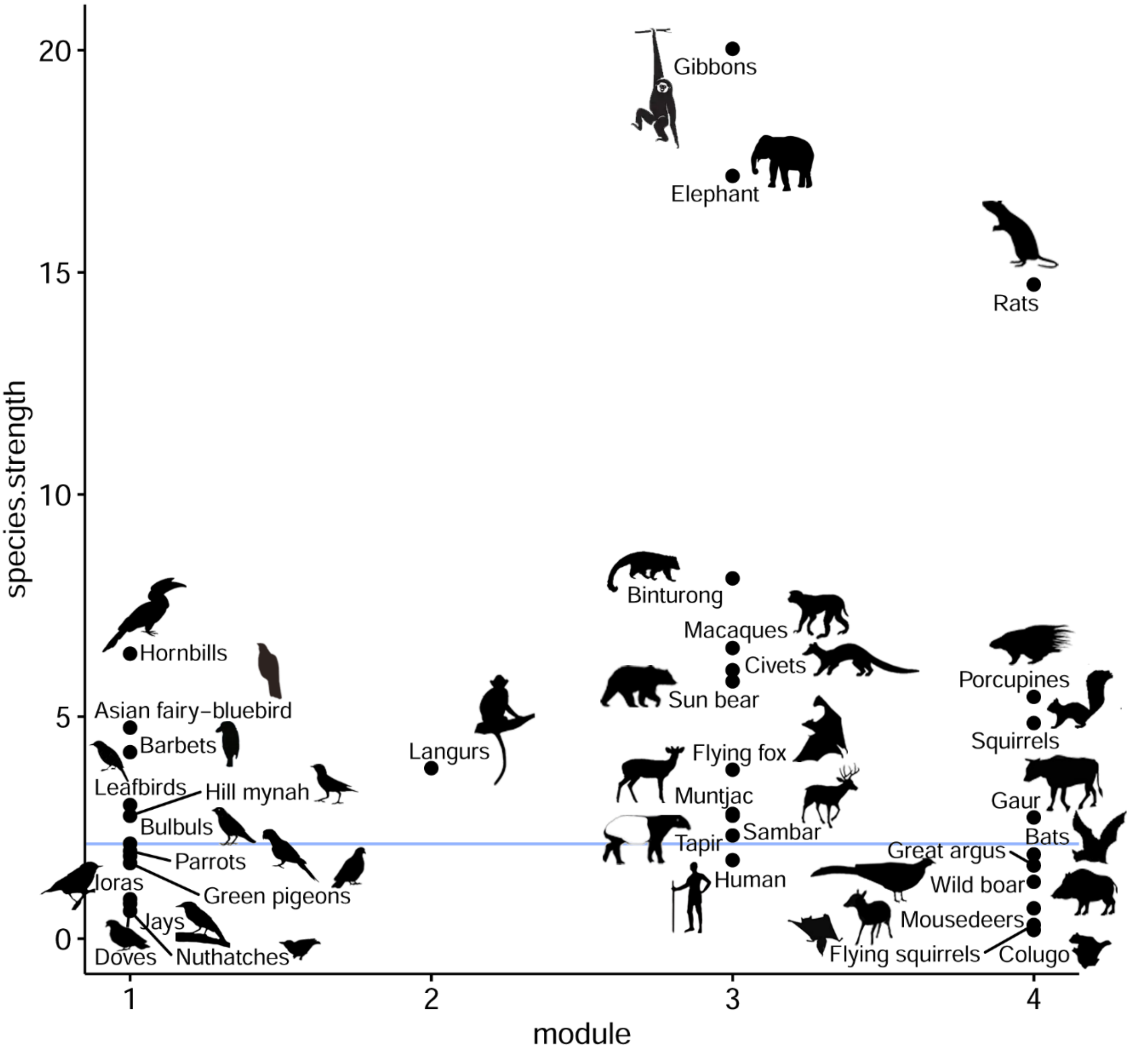


Figure 4.10 Species strength (right) of animals from different modules in the Belum seed dispersal network. The blue line represents the average species strength of all animals (4.3±4.6).

Animal hubs — A hub connects a large proportion of species within a module. *z* values positively correlate with degree (R=0.73, df=32, p< 0.001) (Appendix Fig. A4.22). The average *z* value of animals in the network was 0.0±1.0. In the Belum network, only rats emerged as a hub (*z* ≥ 2.5) (Table 4.18; Fig. 4.11). Nonetheless, I observed animals with distinct *z* values from individual modules. From module one, hornbills, the Asian fairy-bluebird, and barbets had relatively higher z values. From module two, gibbons and the Asian elephant have high *z* values. From module four, porcupine and squirrels have moderate *z* values (Fig. 4.11).

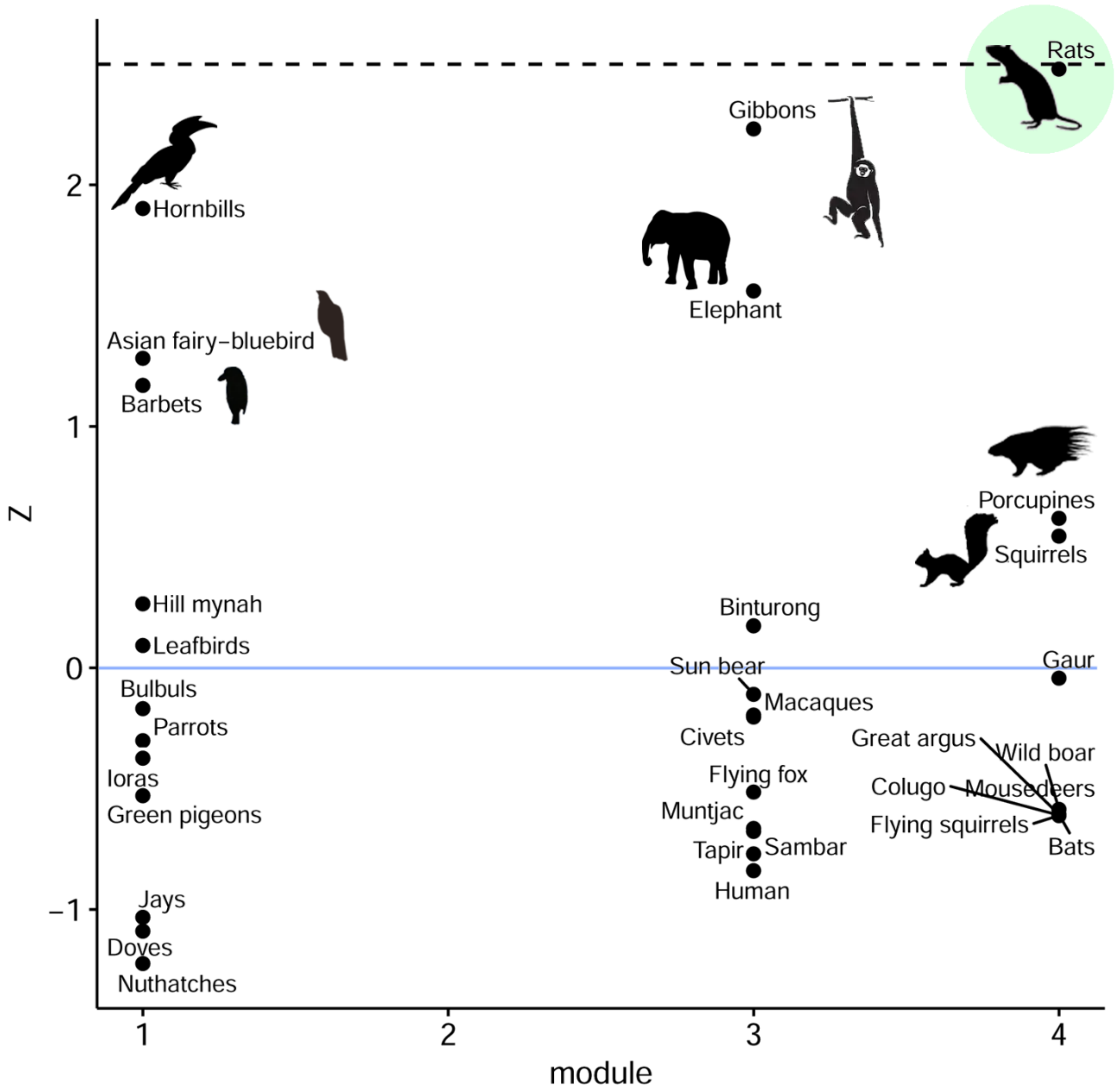


Figure 4.11 *z* values of animals from different modules. The dotted line represents the definition of a hub, i.e., a node with *z* value ≥ 2.5 (Guimerà & Amaral, 2005; Olesen et al., 2007). Rats are the only hub with a *z* value of 2.5. Animals with icons are seed dispersers with high *z* values within its module. The blue line represents the average *z* value of animals (0±0.97).

Animal connectors — A connector links species of different modules. In the network, *c* values did not correlate with degree (R=0.098, df=32, p< 0.58) (Appendix Fig. A4.23). The average *c* value of was 0.32±0.15. Only wild boar emerged as a connector (*c* ≥ 0.62). The Great argus (0.6) had the next highest *c* value (Table 4.18; Fig. 4.12). Within module one, hornbills had the highest *c* value. In module two, langurs had the highest. In module three, macaques and civets had moderately high *c* values. In module four, apart from wild boar and the great argus, mousedeer, gaur, and flying squirrels also had moderately high *c* values (Fig. 4.12).

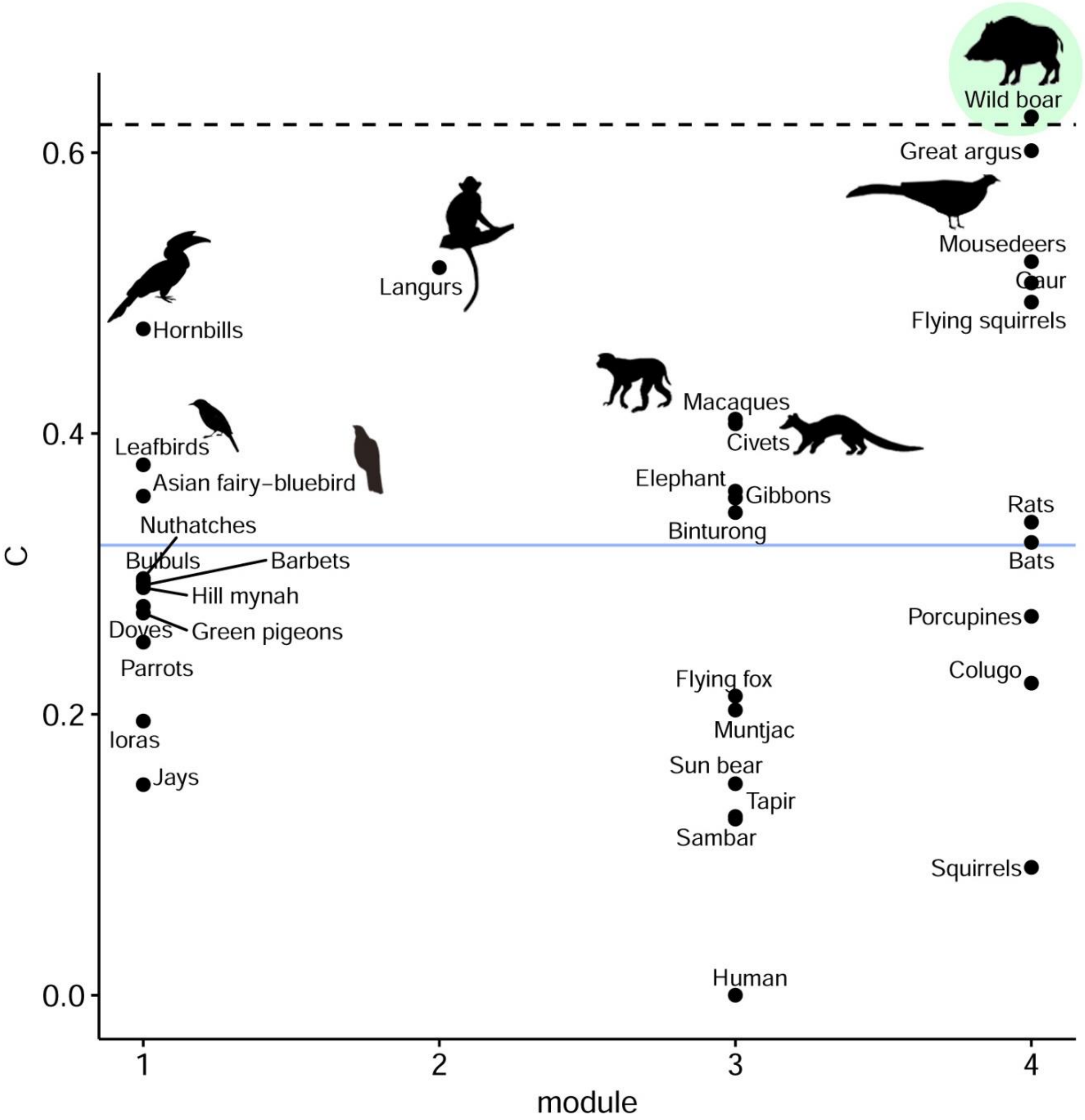


Figure 4.12 *c* values of animals from different modules. The dotted line represents the definition of a connector, i.e., a node with *c* value ≥ 0.62 (Guimerà & Amaral, 2005; Olesen et al., 2007). Animals with icons are seed dispersers with high *c* values within its module. The blue line represents the average *c* value of 0.3±0.2.

Weighted closeness — ‘Closeness’ describes the centrality of a species by its path lengths (node to node) the other nodes in the network (Freeman, 1979). A central disperser would share a greater amount of overlap with other seed dispersers. The average closeness of dispersers was 0.029±0.11. Dispersers most central to the network are gibbons (0.059), binturong (0.05), civets (0.049), the Malayan sun bear (0.043), and macaques (0.041). While helping to maintain robustness, these animals should also be more resilient to random extinctions of species. Less central animals (weighted closeness: 0.012 to 0.020) included porcupines (degree: 31), nuthatches (12), jays (14), doves (12), human (26), flying squirrels (10), rats (70), Malayan tapir (32), and gaur (19) (Table 4.18). On one hand, the seed dispersal functions of these animals may be more vulnerable. On the other hand, a highly linked (e.g. rats) disperser could be helping to maintain dispersal interactions that were vulnerable and peripheral.

Weighted betweenness — ‘Betweenness’ describes the centrality of a species by its position relevant to other nodes in the network and the number of shortest paths passing through it. In the network, weighted betweenness correlate with degree (R=0.46, df=32, p< 0.0064) (Appendix Fig. A4.23. A species with high weighted betweenness has a local niche breadth that is important for the whole interaction system, acting as connectors (Mello et al., 2011). I found that weighted betweenness reflects a species’ importance to the overall network connections, as compared to species with a high *c* value that helps connect a module to plants from other modules. In the Belum seed dispersal network, gibbons thus (0.92) stood out as the most effective seed dispersers. The average weighted betweenness was 0.029±0.16 (Table 4.18). No species had weighted-betweenness close to that of gibbons. Gibbons helped promote functional redundancy in the network as they dispersed plants that are dispersed by multiple species across the network. Their feeding choices thus have a high influence on the seed dispersal phenomena of the system; capable of either promoting or reducing dispersal effectiveness for different plant species of the network and in turn affecting the functional importance of other dispersers.

Plant hubs, connectors, and supergeneralists — Plants that acted as hubs (range 2.5 to 3.9) were *Aidia densiflora* (highest *z* value) from the Rubiaceae family, *Bouea macrophylla* (Anacardiaceae), *Artocarpus rigidus* (Moraceae), *Artocarpus lanceifolius* (Moraceae), *Microcos cf. globulifera* (Tiliaceae), *Garcinia parvifolia* (Ebenaceae) and *Artocarpus elasticus* (fam. Moraceae). Plant connectors were *Desmos* sp. (Annonaceae), *Prunus* sp. (Rosaceae), *four Ficus* spp. (Moraceae), *Microcos cf. globulifera* (Tiliaceae), Burseraceae sp. (Burseraceae), and two unidentified species (Selamak* and Gelimbok*) (Fig. 4.13; 4.14).

A super- generalist is a species that is both a connector and a hub. In the network, no animal emerged as a supergeneralist, but four plant species emerged as super-generalists, three *Ficus* spp. and *Microcos cf. globulifera* (c >0.62, z >0.25). *Garcinia parvifolia* (c =0.61, z =2.6) was a potential super-generalist (Fig. 4.13; 4.14).

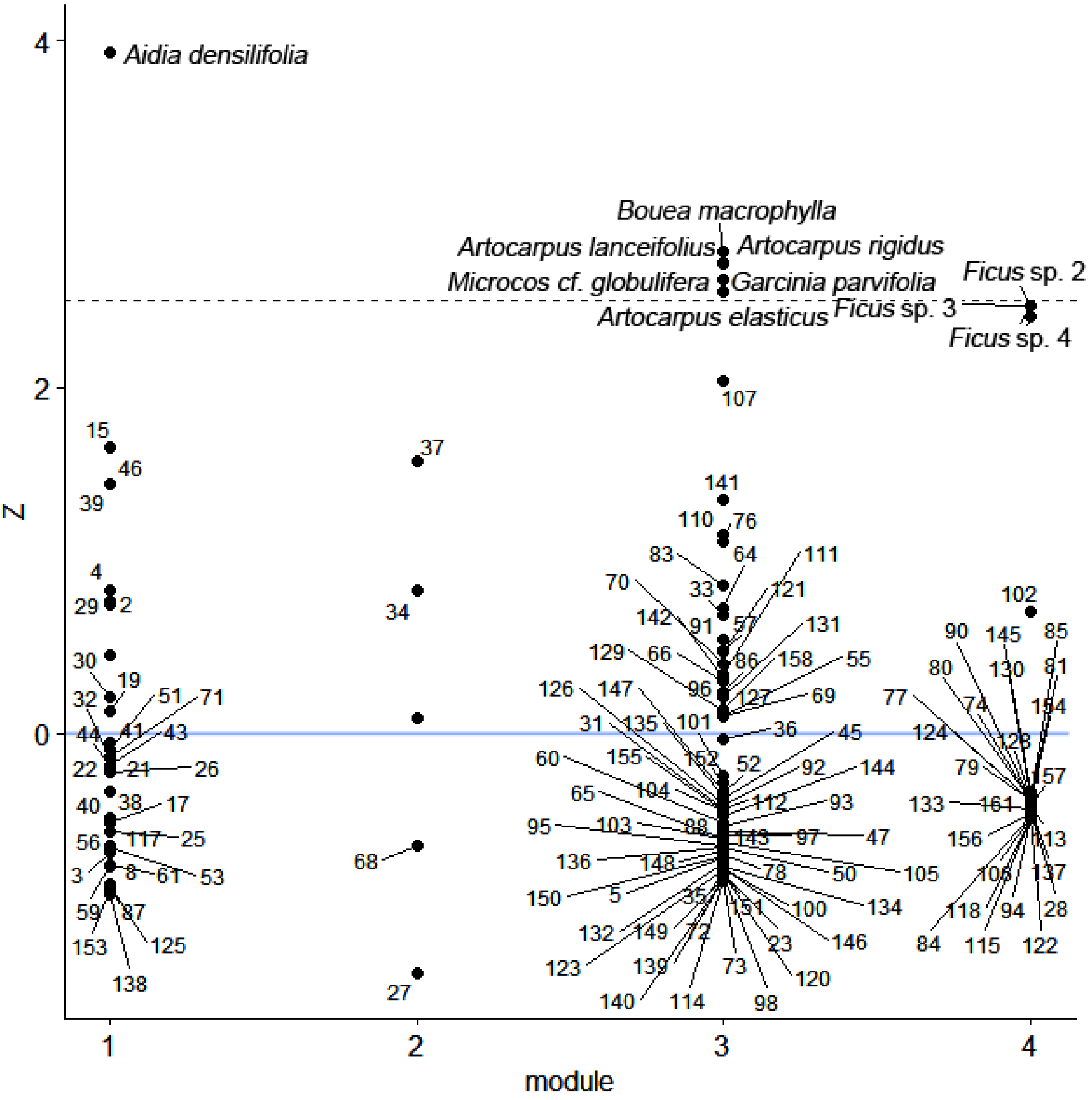


Figure 4.13 z values of plants from different modules. The dotted line represents the definition of a hub, i.e., a node with z value ≥ 2.5 (z value ≥ 0.62) (Guimerà & Amaral, 2005; Olesen et al., 2007). Named plants are hubs. The blue line represents the average z value of plants (0±0.1).

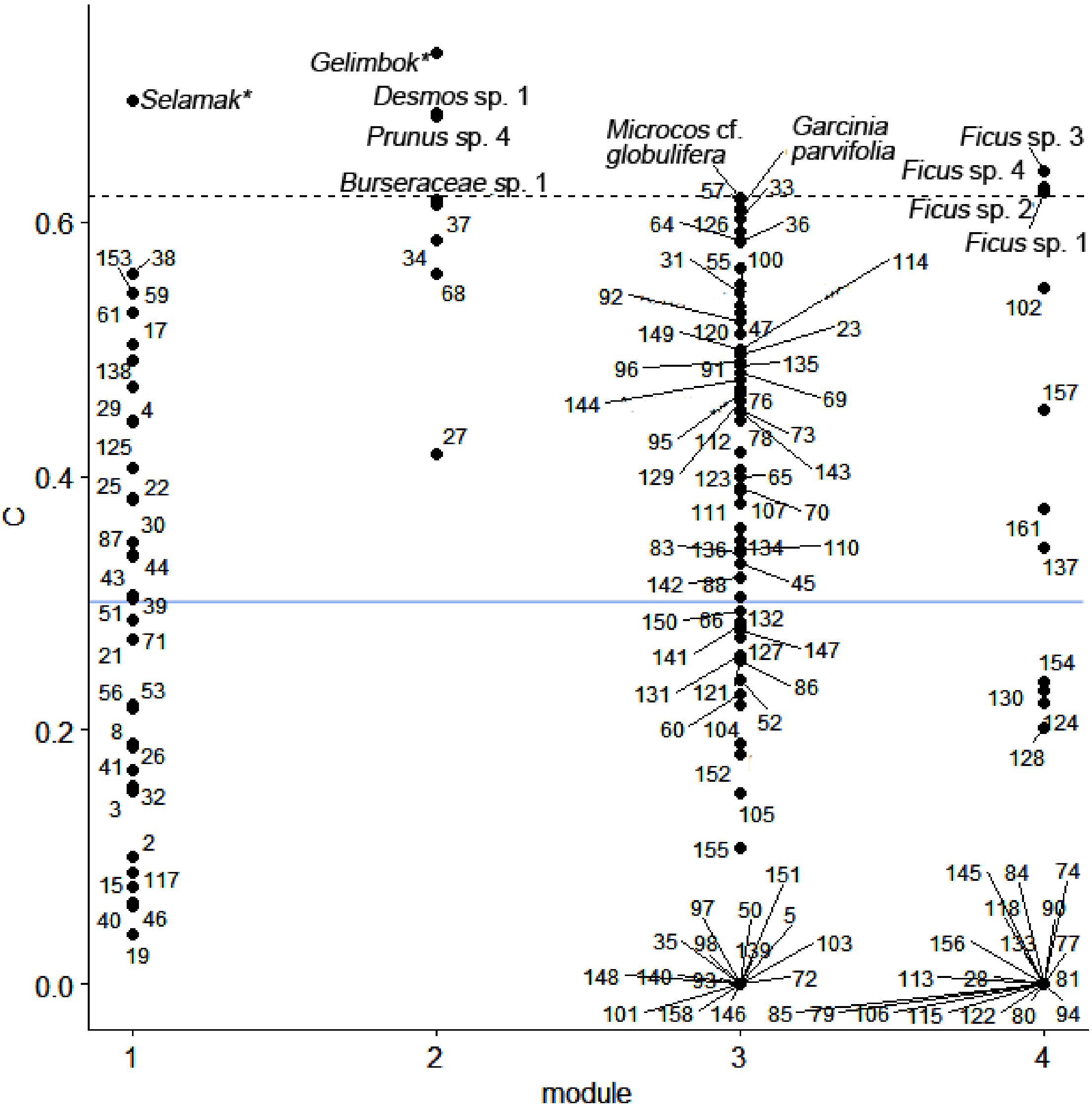


Figure 4.14 *c* values of plants from different modules. The dotted line represents the definition of a connector, i.e., a node with *c* value ≥ 0.62 (Guimerà & Amaral, 2005; Olesen et al., 2007). Named plants are connectors. The blue line represents the average *c* value of plants (0.3±0.2).

Inefficiently Dispersed or Vulnerable Plant Species — I found nine zoochoric plants dispersed by only one or two animals, including five megafaunal syndrome fruits, i.e. fruits with a diameter (dia) larger than 40mm. The plant species are *Citrus macroptera* (90mm fruit dia., 8mm seed dia.; dispersed by gaur), *Diospyros* sp. 4 (60mm fruit dia., 14mm seed dia.; dispersed by binturong), *Diospyros* sp. 5 (57mm fruit dia., 19mm seed dia; dispersed by Asian elephant), *Mezettia cf. macrocarpia* (50mm fruit dia, 30mm seed dia.; dispersed by Asian elephant), Cindros kedik* (50mm fruit dia., 9mm seed dia.; dispersed by Asian elephant), *Gardenia carinata* (23mm fruit dia., 3mm seed dia.; dispersed by macaques), Akar Bod* (11mm fruit dia., 9mm seed dia.; dispersed by the Malayan flying fox), Tahbit* (10mm fruit dia., 8mm seed dia.; dispersed by porcupine), and *Huberantha cf. rumphii* (6mm fruit dia., 5mm seed dia.; dispersed by gibbons).

Principal component analysis (PCA)

I found the largest diameter of seeds dispersed, species strength, weighted closeness, and PDI (generalism) as variables influencing the grouping of modules in the seed dispersal network (Fig. 4.15) (see methods PCA for correlations of other explanatory variables). Most of the variance is accounted for by the first two components. Overall, component one described 62.5% of the variance, component two 28.2%, component three 6.6%, and component four 2.7% of the variance. Between groups, component one accounted for 66.4% and 32.9% of the variance. Within groups, component one accounted for 57.5% of the variance, component two accounted for 31.4% of the variance (Table 4.19).

Table 4.19 Eigenvalues of principal components of the correlation matrix

PC	Eigenvalue	% Variance
Between groups		
1	2.7	66.4
2	1.3	32.9
3	0.03	0.69
Within groups		
1	2.3	57.5
2	1.3	31.4
3	0.29	7.3
4	0.15	3.8
Overall		
1	2.5	62.5
2	1.1	28.2
3	0.27	6.6
4	0.11	2.7

The loadings reflect the extent to which the different variables enter the different components (Hammer et al., 2001). Overall, PC one is moderately correlated with species strength (0.55) and weighted closeness (0.52). PC two is strongly correlated to the largest seed dispersed (0.83). Between groups, PC one is moderately correlated to species strength (0.57) and weighted closeness (0.51). PC two is strongly correlated to the largest seed dispersed (0.79). Within groups, PC one is moderately correlated to species strength (0.55) and weighted closeness (0.54). PC two is strongly correlated with the largest seed dispersed (0.84) (Table 4.20).

Table 4.20 Loadings of principal components of the correlation matrix

PC	**Species strength**	**Weighted closeness**	**Largest seed dispersed**	**PDI**
Between groups				
PC 1	**0.57**	**0.51**	0.26	-0.58
PC 2	0.32	-0.46	**0.79**	0.26
PC 3	-0.03	**0.70**	0.20	**0.68**
Within groups				
PC 1	**0.55**	**0.54**	0.12	-0.62
PC 2	0.33	-0.42	**0.84**	0.08
PC 3	-0.71	**0.46**	**0.52**	-0.14
PC 4	0.29	**0.57**	0.10	**0.76**
Overall				
PC 1	**0.55**	**0.52**	0.25	-0.60
PC 2	0.25	-0.45	**0.83**	0.18
PC 3	**0.76**	-0.40	-0.48	0.16
PC 4	0.22	**0.60**	0.09	**0.76**

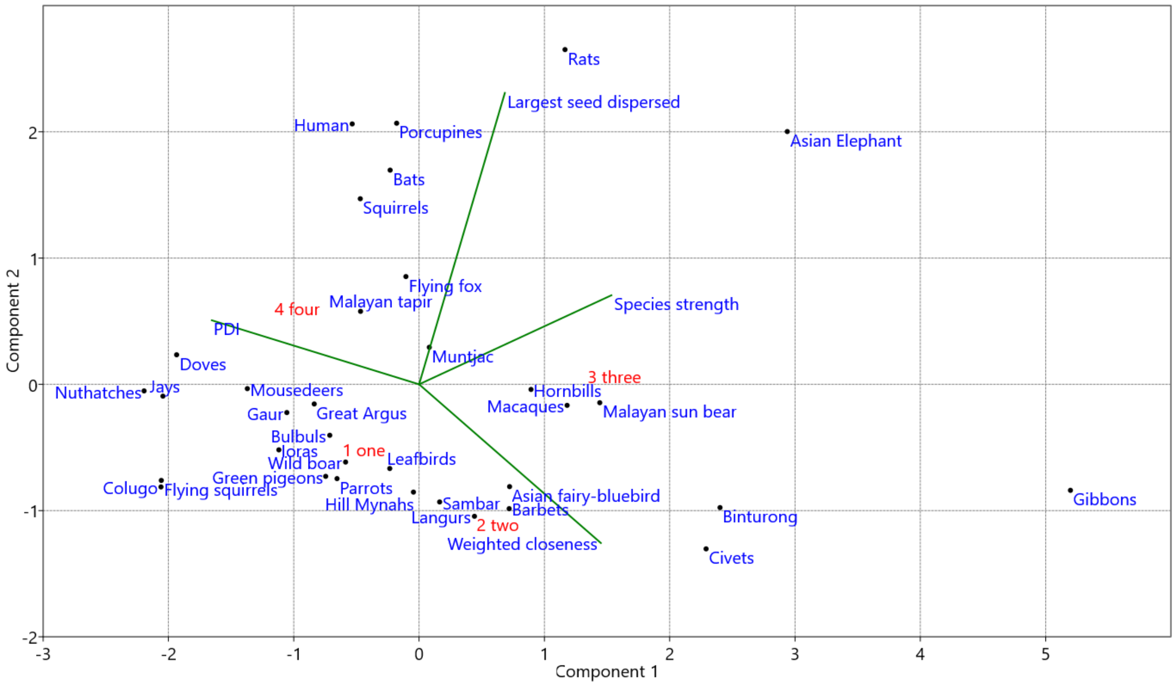


Figure 4.15 PCA plot of the relationship between modules, dispersers, and the four key explanatory variables, i.e., the largest diameter of seed dispersed, species strength, weighted closeness, and PDI.

Module three was associated with weighted closeness, species strength, and moderately to the dispersal of large seeds (Fig. 4.15). It was negatively associated with PDI (high PDI = specialism). Animals in module three, thus, included a group of highly-connected and central seed dispersers with high species strength, and some were important for the dispersal of large seeds. Module two was associated with weighted closeness. It was also negatively associated with PDI and the largest seed dispersed. Animals in module two, thus, disperse small-seeded plants that are central to the network. Module one was negatively associated with the dispersal of large seeds and species strength. Its dispersers spread out between PDI and weighted closeness. Animals in module one thus dispersed small seeds and had low species strength in the network. Some dispersers were more specialised and less central, while some dispersers were more central and less specialised. Animals in module four were associated with PDI and the largest seed dispersed. Animals in module four were thus specialised dispersers that helped disperse large seeds. Only rats lean towards high species strength in the module.

Between groups, animals with the highest scores for PC one were gibbons (5.2), the Asian elephant (3.0), binturong (2.4), and civets (2.2). Animals with the highest scores for PC two were rats (2.7), porcupines (2.0), the Asian elephant (2.0), and humans (2.0) (Table 4.21). Within groups, animals with the highest scores for PC one were gibbons (5.3), Asian elephant (2.7), binturong (2.5), and civets (2.4). Animals with the highest scores for PC two were rats (2.8), porcupines (2.4) the Asian elephant (2.1), and humans (2.0). Overall, animals with the highest score for PC one were gibbons (5.2), the Asian elephant (2.9), binturong (2.4), and civets (2.3). Animals with the highest score for PC2 were rats (2.7), porcupines (2.1), human (2.1), and the Asian elephant (2.0). Refer Appendix Table A4.3 to A4.5 for a complete list of PCA scores.

Table 4.21 Between-group scores of the correlation matrix for PC 1 and PC 2 (arranged according to scores: high to low); in green (top 3), in yellow (top 10). See Appendix Table A4.2 for complete details

Animals	PC 1	Animals	PC 2
Gibbons	5.2	Rats	2.7
Asian Elephant	3.0	Porcupines	2.0
Binturong	2.4	Asian elephant	2.0
Civets	2.2	Human	2.0
Malayan sun bear	1.4	Bats	1.6
Rats	1.2	Squirrels	1.5
Macaques	1.2	Malayan flying fox	0.8
Hornbills	0.9	Malayan Tapir	0.5
Asian fairy-bluebird	0.7	Doves	0.3
Barbets	0.7	Southern red muntjac	0.2

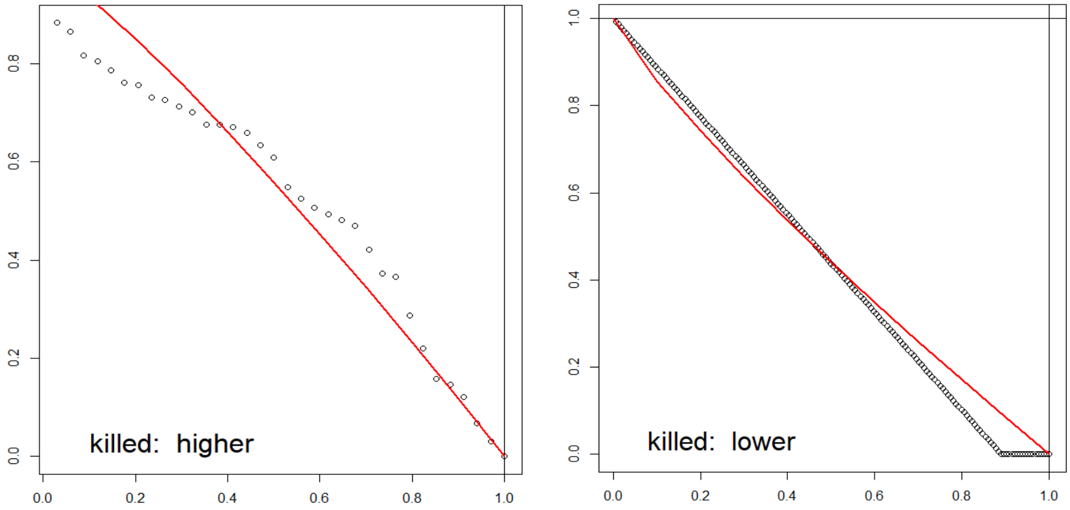
Amongst animals of high scores, I found animals strongly correlated to gibbons were hornbills (1.0), binturong (0.9), the Asian fairy-bluebird (0.9), civets (0.9) and macaques (0.9), barbets (0.8), the Malayan sun bear (0.8) and the Asian elephant (0.7). Animals strongly correlated to the Asian elephant are hornbills (0.8), rats (0.8), and gibbons (0.7). Animals strongly correlated to binturong include civets (1.0), macaques (1.0), the Asian fairy-bluebird (1.0), barbets (1.0), gibbons (0.9), hornbills (0.9), the Sambar deer (0.8) and langurs (0.8). Animals strongly correlated to rats include porcupine (0.9) and the Asian elephant (0.8). Porcupine was strongly correlated with Malayan tapir (0.9), the Malayan flying fox (0.9), human (0.9), rats (0.9), and squirrels (0.8). Refer Appendix Table A4.6 for a complete list of correlation values.

Defaunation

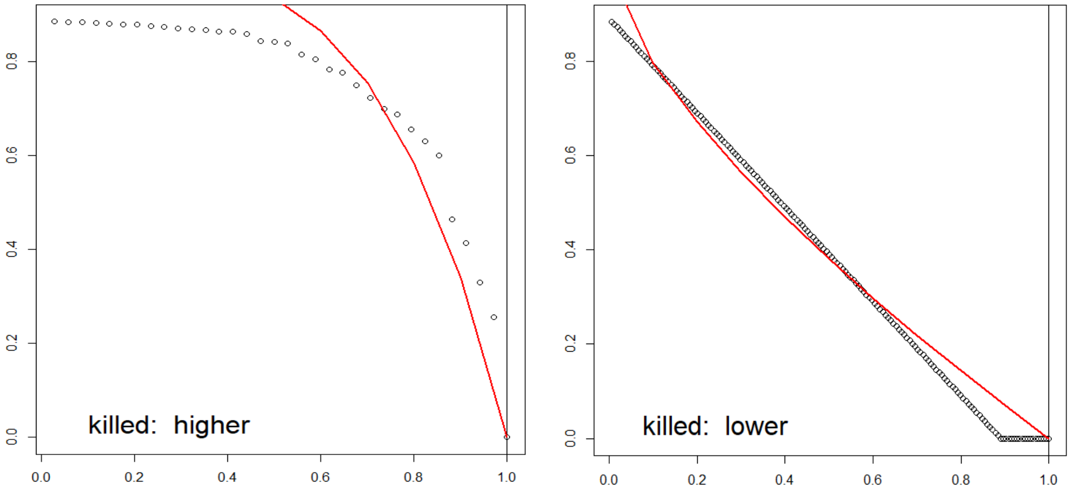
I found that the loss of highly connected species can cause seed dispersal networks to be less robust to extinction across the entire plant and animal communities. The removal of seed dispersers by three different algorithms resulted in different extinction patterns (Fig. 4.16). The random loss of species resulted in an initial slow loss of plant species followed by an accelerating decline after 50–60% of the dispersers were lost (exponent animal: 3.6). The loss of the most specialised seed dispersers resulted in a much slower loss of plant species where plant species start to decline sharply when 70% of the dispersers were lost (exponent animal: 6.6). The elimination of highly connected species led to the rapid secondary extinction of both plant species, as compared to both random extinction and the loss of specialised species (exponent animal:1.2). The simulated extinction curve showed rapid secondary extinctions of both plant species instead of a period of stability, as observed with the random loss of species (Fig. 4.16).

Removing plants with three different methods resulted in similar linear extinction patterns, where animals go extinct rapidly following plant loss. However, the extinction slope for the removal of the most connected to least connected plants was steeper (exponent plant: 0.8), than the systematic loss of the most specialised plant species (exponent plant: 0.7) and the random loss of plant species (exponent: 0.69).

Loss of the most connected to least connected animals and plants.



Random loss of species



Loss of least connected to most connected animals and plants.

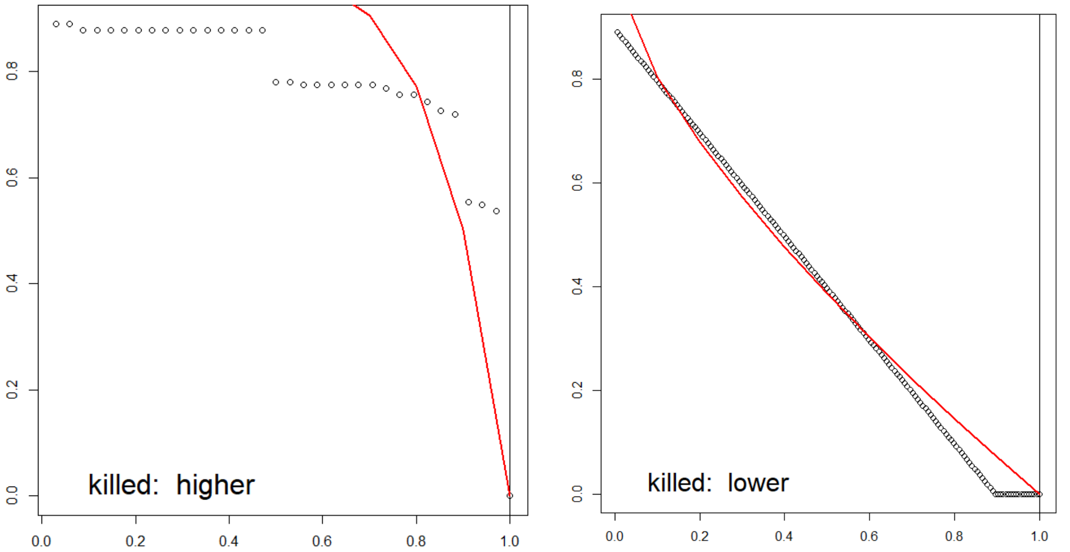


Figure 4.16 Coextinction of animals (left) and plants (right) in the loss of highly connected species (top), random extinctions (middle), and loss of rare species (bottom).

DISCUSSION

In this study, I explored the seed dispersal system of a tropical rainforest with a high diversity of megafauna and frugivores, through a combination of field observations, measured fruit traits, local ecological knowledge (LEK), and published records. This network is the first community-wide seed-dispersal network from a Sundaic forest. I used key network metrics to detect the species that were important to the seed dispersal network of the Royal Belum rainforest.

The Belum Seed Dispersal Network Structure

The structure of a network determines its robustness. High diversity in the seed dispersal network of Belum established its modular (0.289), nested (26.3), connected (0.142) and generalised (0.225) properties; these are features that support persistence in ecological systems (Memmott et al., 2004; Olesen et al., 2007; Thébault & Fontaine, 2010; Stouffer & Bascompte, 2011; Grilli et al., 2017; Nogales et al., 2016). As a result, both the plant and animal communities were highly robust to random extinctions (animal robustness: 0.82, plant robustness: 0.96).

Distinct modules are observed within local networks when the overlap in the plants dispersed among animals is low (Mello et al., 2011). In the Belum network, sub-communities of plants and their seed dispersers were segregated into four modules (Newman & Girvan, 2004; Thébault, 2013). This included a module of birds and 34 plant species, a module represented solely by langurs and eight plant species, a module comprising intermediate to large-bodied mammals (Table 4.17: body weights) and 74 plant species, and a module that included rodents, smaller bats, some less generalised mammals, and 30 plant species.

'Modularity' measures the strength of nodes within and between modules in a network. Networks with high modularity have dense connections within modules and sparse connections between nodes of different modules (Kashtan & Alon, 2005; Bascompte & Jordano, 2014). The Belum network has a modularity of 0.289, within the value of existing networks (ranging from 0.05 to 0.6). Afrotropical systems have a median of around 0.35 (range 0.2—0.6) and neotropical systems around 0.4 (range 0.2—0.6) (referenced from Schleuning et al., 2014; Dugger et al., 2018).

Network hubs (z value ≥ 2.5, c value < 0.62) and connectors (c value ≥ 0.62, z value < 2.5) are important for promoting modularity and defining the structure of the network. In the Belum network, only rats that were represented by a large taxonomic group emerged as hubs.

Langurs were exclusively assigned to one module; hence, no *z* value was computed. With only one animal network hub, seed dispersers with a high within-module degree (*z* values) from the various modules, i.e. hornbills in module 1, gibbons and elephants in module 3, were important to the structure of the module observed. Highly-linked species have a higher inclination or probability of joining other nodes, which is known as the 'preferential attachment' (Newman, 2001; Jeong et al., 2003; Bascompte & Jordano, 2014). These nodes tend to cluster together and are thus important for the formation and cohesion of modules (e.g. Silva et al., 2015; Nogales et al., 2016). 'Rats' and 'hornbills', however, are taxonomic groups comprising multiple species (Table 4.1), and the importance of some species within the group is likely to be amplified. In the network, several animals were similarly represented by a taxonomic group of more than two species (Table 4.01). Collectively these groups are important to the network, but caution is required when interpreting the importance of individual species from this network. Amongst rats (Table 4.2), the long-tailed giant rat (*Leopoldamys sabanus*) is a likely candidate for the high *z* value (further discussed under 'rats and other rodents' section). Amongst hornbills, the Great hornbill and Wreathed hornbill are likely dispersers with high *z* values (further discussed under 'birds and the importance of hornbills'; sensu Naniwadekar, 2019). These species are relatively large within the taxonomic groups and may have the potential to disperse a higher diversity of seeds (Mueller et al., 2014; Naniwadekar et al., 2019).

Although I could not test for the association of the modules with non-quantitative variables in the PCA, I found the important animals with high *z* values were also animals involved in the most seed dispersal interactions from different forest strata and animal guilds — i.e., birds, arboreal and terrestrial mammals, and rodents (tables 4.12—4.15). In the seed dispersal network, hornbills represented 5% of the total network interactions (1229), which was the highest amongst birds. Gibbons (7.2%), was the highest amongst arboreal mammals, and the Asian elephant (6.5%) was the highest amongst terrestrial mammals. The taxonomic group "rats" (5.7%) had the most dispersal interactions amongst rodents. I thus associate the primary mechanism underlying network modularity and the assignment of modules as niche partitioning (Tillman, 2004; Levine & HilleRisLambers, 2009; Tang & Zhou, 2011) between seed dispersers from different forest strata and guilds (Schleuning et al., 2011). In highly diverse systems, such as occurs in Royal Belum, competition among frugivores for shared resources can be reduced by the selection and use of different plant species (i.e., resource partitioning; Tillman, 2004; Levine & HilleRisLambers, 2009; Tang & Zhou, 2011). Hence, the modules observed reflect the grouping of frugivores according to their niche breadth as a result of diet and habitat specialization (Schleuning et al., 2011). Further differentiation of modules was related to how efficient (indicated by species strength, *z* values, and degree), central (weighted closeness, weighted betweenness), and specialised (PDI) the seed dispersers were, as reflected by the PCA results. PC1 explained for 66% of the variance between groups and was represented by dispersers with high species strength (between groups PC1 loadings: 0.57) and weighted closeness (between groups PC1 loadings: 0.51). PC 2 explained 33% of the variance and was represented by the largest seed dispersed (0.79) and species strength (loadings 0.32).

Module 3, the module with arboreal and terrestrial mammals, was associated with PC 1 and PC2. It comprised highly-linked and effective seed dispersers (species strength), animals that dispersed a large proportion of fruits that were commonly utilised and dispersed by central species (centrality: weighted closeness; refer Table 4.17), and animals that dispersed the largest seeds (e.g. Asian elephant, human, Malayan flying fox, and Southern red muntjac) (Table 4.20 and 4.21; Fig. 4.15). Module one was negatively associated with PC 1 and PC 2. Apart from hornbills, Asian fairy-bluebird, barbets and doves, most birds had low species strength and were specialists of small-seeded fruit species. Module two was associated with weighted-closeness and negatively associated with PC2, dispersing small-seeded seeds that overlap with central species. Module four comprised of specialised dispersers of large seeds that are rarely dispersed by most species.

Animals that connect modules in the network include the network connector wild boar and also the animals with high *c* values within their respective modules such as hornbills, langurs, macaques, and civets. In module one, the taxa "hornbills" constitutes multiple species. Network connectors (*c* value above 0.62, *z* value below 2.5) are not necessarily highly linked species within their module (Olesen et al., 2007), as they serve to connect other modules. Any hornbill species thus have the ability to fulfil this role. In module three, civets formed a larger taxonomic group (at least 4 species); thus macaques (represented by 2 species) appeared as the more prevalent connector (Fig 4.12; Table 4.18). The extinction of network connectors could result in a less cohesive network, or modules that could become more isolated (Olesen at al., 2007); this theory is yet to be advanced in ecological studies. In module four, I found many animals such as the great argus (degree: 14), mousedeers (5), gaur (17), and flying squirrels (5) with high *c* values. The great argus and gaur were likely to be contributing to network connectivity. However, a low degree in mousedeers and flying squirrels could have resulted in the calculations of high *c* value. Instead of being network connectors, I deduced that these animals were instead exhibiting a weak seed dispersal service. The presence of network nestedness promoted the persistence of these poorly-connected species through indirect connections to the more stable generalised species and module (Bascompte et al., 2003; Carlo & Yang, 2011).

In the Belum network, I found all animals were specialists (ranging from 0.80 to 0.98) according to PDI measurements (PDI 0 = perfect generalist, PDI 1 = perfect specialists), although many were highly linked. This is the result of proportional interaction in a highly diverse network. This could confuse the broader definition that referred generalists as animals with a broad diet range, i.e. highly-connected species. To avoid confusion, I described animals as highly-connected or less-connected. To link with existing concepts, I may refer to highly-connected animals as generalised animals, and less connected animals as specialised animals. Future studies may provide a clearer definition of generalist and specialist in highly diverse networks and ecosystems.

Nestedness is a key feature of the network that promotes resilience to functional extinction. In a nested network, asymmetric specializations and the effects of preferential attachment characterize the network. With the presence of asymmetric specializations, the majority of the species are less-connected specialists. Only a few generalists will emerge out of the network (Bascompte & Jordano, 2014). These highly-linked species (network nodes) are inclined to connect more nodes, as described earlier as the effects of 'preferential attachment' (Newman, 2001; Jeong et al., 2003; Bascompte & Jordano, 2014). The presence of asymmetric specializations and preferential attachment thus makes a few species exceptionally important to the network. In the Belum network, the effects of preferential attachment could be associated with the efficiency of dispersal, such that an efficient seed disperser tends to facilitate seed dispersal for more plant species.

In the seed dispersal network, I thus associate gibbons and the Asian elephants as the highest-connected species with the highest species strength and of exceptional importance to the system. The core assemblage of seed dispersers also included relatively highly-connected dispersers such as binturong, macaques, civets, and sun bear that carried high network weights (Fig. 4.06 and 4.07). These animals were assigned in the same module and dispersed a diverse range of fruit species both within and out of the module (module three). Interactions within the core of the nested network promoted cohesion, while interactions out of the module help maintained connectance (based on Bascompte et al., 2007). Such diverse interactions help increase network nestedness and the overall stability of the network as generalised seed dispersers were held tightly within the module through short path-lengths. At the same time, these highly-connected species were linked through their plant partners to more specialised species such as nuthatches, jays, colugos and flying squirrels within other modules, thereby reducing the chances of extinction of specialised species (Bascompte et al., 2003; Carlo & Yang, 2011). Through increasing network nestedness, generalised species thus help prevent network disassembly and promote persistence (Memmott et al., 2004; Bascompte & Stouffer, 2009; Nogales et al., 2016). Removing a poorly-connected species linked to the generalised assemblage will introduce little impact to the overall network. Removing generalised species could make a network more vulnerable to disassembly than random extinctions (Palacio et al., 2016).

Like many other network metrics, nestedness is a secondary covariate rather than a causative factor (James et al., 2012). They are structures or properties that arise as a result of the pattern of interactions amongst nodes. More work is needed to explore the relationship between these network metrics using different methods to derive a more accurate description of the network (Bascompte & Jordano, 2014). Simpler metrics that accompany network analysis (e.g., number of mutualistic partners a species has) could help determine the mechanisms driving higher-order network properties (James et al., 2012). To assess species' importance or the consequences of their extinction, biological attributes of the precise identity must be examined (e.g., phylogenetic signals). To have a better insight into how the seed dispersal function is mapped into the network, I shall discuss the functional attributes of selected species, beyond the computation of network metrics.

Functionally Important Species

The methodologies for defining 'keystone species' are not well-established (Jordán et al., 2009; Stevenson et al., 2015; Cagua at al., 2019), but most studies have recognized the importance of generalised species (González et al., 2007; Palacio et al., 2016; James et al., 2017). Reviewing 43 studies that encompassed five main habitats — deciduous, evergreen, rainforests, montane forests, and the Atlantic forest, from different geographic regions (Neotropical, Afrotropical, Oriental, and Oceanian), Escribano-Avila et al. (2018) found 11 studies that identified important species to the networks. These are either species that served as network or module hubs, connectors, species belonging to the central core, or species with a high degree; and were referred to as keystone seed dispersers. From the analysis of 15 seed dispersal datasets (seven bird and eight bat networks) from the Neotropics, specialised frugivores that are highly dependent on fruits in their diet were found as the only seed dispersers with high centrality and were proposed as possible keystone species (Mello et al., 2015). This is supported by Escribano-Avila et al., (2018) who found obligate frugivores and large animals (e.g. cracids, rodents, monkeys, megafauna) as keystone animals. The fundamental definition of a keystone species is 'a species whose impacts on its community or ecosystem are disproportionately larger than expected from its biomass or abundance (Paine, 1969; Heywood, 1995). Keystone species can be rare or common, dietary generalists or specialists that promote ecological complexity and stability (Strauss, 1991; Bond, 1994). Terborgh (1988) suggested that seed predators are kept in check by carnivores. The elimination of carnivores may result in shifts of forest composition to smaller-seeded species. Extending these concepts to network studies, keystones species could be identified as functionally important species whose loss may lead to shifts in the seed dispersal dynamics. This network allowed us to identify functionally important seed dispersers.

Animals important to seed dispersal network structure — As previously discussed, hornbills, langurs, gibbons, the Asian elephant, and rats (multi-species hub) were essential to maintaining the hierarchical structure of the different modules in the network. Supported as important dispersers from other studies, large-bodied species (Mueller et al., 2014) such as the Great hornbill and Wreathed hornbill could be key dispersers amongst hornbills (Naniwadekar, 2019), and the long-tailed giant rat (*Leopoldamys sabanus*) could be a key disperser amongst rats (Table 4.2) (Yasuda et al., 2000, Cheng et al. 2005). Wild boar (a network connector), hornbills (could include less-connected species), langurs, and macaques were species important to the connection of these modules. Gibbons, the Asian elephant, binturong, macaques, sun bear, and rats were species with the highest species strength, indicating high dependence of plants on these animals for seed dispersal. Rats and hornbills were large taxonomic groups with high species strength. Gibbons, the Asian elephant, binturong, civets (as a large taxonomic group), and sun bears were important to the maintenance of network nestedness, helping to increase the network's resistance to seed dispersal functional co-extinctions.

Gibbons, the most efficient seed disperser — Being the most effective and central seed disperser (highest weighted betweenness), gibbons held large control capacity over the seed dispersal network (Freeman, 1979; Estrada, 2009; Cagua et al., 2019). Gibbons promote functional redundancy of the overall system, but their functional role is disproportionate and is irreplaceable by another species. They are dispersers with the highest species strength (influence on plants), highest z value after rats (as a large taxonomic group), and dispersers with the highest score in the PCA component that helped describe the overall mechanism driving the network pattern. The loss of gibbons could lead to higher numbers of lower quality seed dispersal interactions or the re-structuring of the central roles within the network.

Small-bodied gibbons are "true frugivores" that may spend more than 60% of their feeding time on fruits (>20% on figs) and who use keystone figs as a fallback resource (Elder, 2009; Marshall et al., 2009; McConkey, 2009). Amongst primates, they are effective seed dispersers who swallow most seeds whole, dropping and destroying few seeds they handled and dispersing most seeds more than 100m away from parent trees (McConkey & Chivers, 2007; McConkey, 2009). In Borneo, a group of gibbons can disperse up to 81% of the species they consume, over 16,400 seeds/ km^2 (McConkey, 2000; McConkey et al., 2002). As upper canopy dwellers, seeds defecated by gibbons are often scattered as they fall through leaves. In comparison to the clumped deposition that faces harmful consequences from density-dependent pathogens or predators, germination success is usually higher in such scattered seeds (Howe, 1989; Corlett, 1998; Albert et al., 2013).

Gibbons dispersed a high diversity of plants which were also dispersed by other animals, thereby promoting redundancy in the system. Where functional redundancy exists, species within guilds deliver similar ecological services. With the disappearance of some interactions, a plant thus has alternative dispersers that could help ensure its persistence. In seed dispersal, redundancy can only be achieved if animals disperse seeds to safe sites, at a relatively similar distance away from the parent plant. This requires similar foraging and ranging patterns between the seed dispersers, and fruits to be a limiting resource (McConkey & Brockelman, 2011). While gibbons increase the resilience of the network by promoting functional redundancy of the overall system, its functional role is irreplaceable. Gibbons have the potential to replace the role of inefficient seed dispersers (McConkey & Brockelman, 2011). The opposite may see a decline in the overall effectiveness of the seed dispersal interactions. In comparison to a poorly connected species, the disappearance of a highly connected and efficient species would lead to less effective dispersal of many plants. Plants dispersed by gibbons would rely on multiple alternative dispersers, some less efficient, to maintain the seed dispersal service. The absence of gibbons may possibly lead to changes to the overall system and shifts in the seed dispersal dynamics.

Gibbons - Asian elephant complementary seed dispersal

With further assessments through PCA, I found the Asian elephant to provide a complimentary seed dispersal role compared to gibbons. While both dispersers overlap in resource use (consuming 60 and dispersing 50 similar plant species), their combined seed dispersal abilities due to different forest-strata specialization help promote variability (seed sizes dispersed), functional redundancy (overlapping dispersed species), and enhanced resilience to the overall seed dispersal system, driving stability to the seed dispersal function.

Forest strata and seed dispersal differentiation — Gibbons are highly frugivorous seed dispersers that feed within plant crowns in the canopy and sub-canopy strata (McConkey, 2000; Chanthorn, 2017), while the Asian elephant is the largest terrestrial seed disperser (Campos-Arceiz & Blake, 2011). Gibbons can be selective in their diet selection when fruits are abundant. If primates are constrained to specific routes, they may contribute to habitat modification with their feeding behaviour (Chapman et al., 2013). Repeated visits to the preferred food sources increase the chance of seeds of other species being deposited under the feeding tree, thus facilitating species richness in the neighbourhood (McConkey, 2000; Asensio et al., 2011; Chanthorn, 2017). The Asian elephant is a generalist species capable of dispersing at least 122 fruit species from 92 genera and 39 families (Campos-Arceiz and Blake 2011), although fruits are not their principal diet (see chapter two). In the Sundaic rainforest, while the Asian elephant can be effective dispersers for some fruits, finding and removing fresh fruits from fruiting trees can be rare (e.g. 1.4% of visits to *Irvingia malayana* as compared to 24.4% of visits by wild boar) (Ong et al., 2019). Both gibbons and Asian elephants are highly efficient seed dispersers who swallow seeds intact. Gibbons disperse seeds over medium distances beyond 100m (25% > 100m, range: 0–138m; McConkey & Brockelman, 2011) away from the parent plant. The Asian elephant can remove seeds in bulks, and disperse them over long distances from 1.2 km (median 1.2km, mean 1.2–2.1km, max. 5.8km; Campos-Arceiz et al., 2008) to around 10 km (Sekar et al., 2015). The seed sizes (median=11, mean=13±9, min.=1, max.=47; N=79) dispersed by the Asian elephant cover sizes beyond the range (median=8, mean=9±5, min.=1, max=22; N=87) dispersed by gibbons, several of which are megafaunal syndrome fruits (Sekar, 2014). Such complementary strategies were observed to contribute to effective seed dispersal of *Garcinia benthamii* in Khao Yai National Park, Thailand (McConkey et al., 2015).

Network contribution by gibbons and the Asian elephant — Gibbons and the Asian elephant were the most important seed dispersers for network nestedness. Both have the potential to drive the seed dispersal patterns tied with the specialist species (plants and indirectly animals) attached to them (based on Bascompte & Jordano, 2014). Being highly adaptable to spatiotemporal resource variability, their complementary seed dispersal behaviour created a module that encompassed highly diverse interactions, sharing correlations with different seed dispersers. As reflected in the PCA, gibbons overlapped in their dispersal roles with hornbills (1.0), the Asian fairy-bluebird (0.9), and barbets (0.8) from module one, and langurs (0.6) from module two. The Asian elephant overlapped in their dispersal role with rats (0.8) and porcupines (0.5) in module four, and hornbills (0.8) in module one. Within module three, gibbons were more strongly associated with binturong (0.9), civets (0.9), macaques (0.9), Malayan sun bear (0.8) and the sambar deer (0.6), while the Asian elephant was closer to dispersers with high species strength such as binturong (0.5). Both gibbons and the Asian elephant are relatively strongly (0.7) correlated in their dispersal roles.

The Asian elephant as a seed dispersal functional generalist

The Asian elephant played a generalist role in its seed dispersal function and was important for enhancing dispersal variability in the network. Results from PCA showed that Asian elephants had a strong association with both PCA components, i.e. (i) dispersers with high species strength and central species, and (ii) the dispersers of the largest seeds. Between groups, gibbons, the Asian elephant, binturong, civets, and sun bear had the highest score for PCA component one (66.4% between-group variance). Rats, porcupines, Asian elephants, humans, and bats had the highest score for PCA component two (32.9% between-group variance). The importance of Asian elephants in both niches (as represented by PCA components) indicated their functional role in ensuring the diversity of plants and fruit traits in the community.

Dispersers of large seeds: rats and the Asian elephant — Earlier, I surmised the complementary seed dispersal roles played by gibbons and the Asian elephant. Here, I found that both rats (multi-species taxonomic group) and the Asian elephant were associated with the dispersal of the largest seed. Results from PCA showed PC 2 (33% of the variance) was represented by the largest seed dispersed (loadings 0.79) and species strength (loadings 0.32). Rats were more strongly associated with PC 2 (between-group scores 2.7) than the Asian elephant (between-group scores 2.0). However, both species had dispersed the same diameter of the largest seed (46.9mm) in the network. Strong associations of rats with PC 2 was likely due to lower species strength (14.7) and lower association with PC 1 (score 1.2) in rats as compared to the Asian elephant (species strength 17.2, PC 1 score 3.0).

From the Belum network dataset (N=164 plant species), 39 (24%) seeds dispersed by rats, and 35 (21%) seeds dispersed by the Asian elephant were above mean seed size (11mm). Both rats and the Asian elephant dispersed approximately the same number of plant species with seed diameter above 15mm (rats =24, 15%; elephant =23, 14%), and plants with seed diameter above 20mm (rats =15, 9%; elephant =14, 9%). Nonetheless, there are strong differences in their ability for the dispersal of the megafaunal syndrome fruits as explained in the next section. In module three, the next largest mammal, i.e., the Malayan tapir (disperses seeds up to 25.7mm) and Malayan sun bear (28.2mm) are also important for swallowing large seeds, but the dispersed seeds were relatively smaller than the Asian elephant and rats.

Between the Asian elephants and rates, there are major differences in dispersal distance and seed handling which are important for the seed dispersal outcome. Asian elephants are long-distance seed dispersers that could transport seeds around 1 to 2km (median 1.2km, mean 1.2–2.1km, max. 5.8km) in a rainforest-like Belum (based on Campos-Arceiz et al., 2008), while seeds dispersed by rats are moved over short-distances. In Pasoh, the long-tailed giant rat and *Maxomys* spp. were observed scatter-hoarding seeds. Although the caches were quickly retrieved within a day (78.7%), the long-tailed giant rat removed seeds up to 29m away from the feeding platform (range 0.4–29.4m; mean 16.1m) (Yasuda et al., 2000). From China, seeds dispersed by Edward's long-tailed rats were recorded at around 2.4m (Cheng et al., 2005), and mostly less than 20m by the large Japanese field rat (*Apodemus speciosus*), Chinese white-bellied rat (*Rattus confucianus*) and striped field mouse (*Apodemus agrarius*) (Li & Zhang, 2003). Elephants swallow large fruits efficiently and transport them in bulk (Babweteeraa, Savill & Brown, 2007). Rats could effectively forage for scattered seeds across broad resource patches such as at the edges of seed shadows (Smythe, 1986; Janson & Emmons, 1990; Beck & Terborgh, 2002). This complements elephants that more often travelled on foraging paths (based on African forest elephant, Short 1981; Vanleeuwé and Gautier-Hion; 2002; and personal observations), such that seeds may be more successfully dispersed along main trails, clearings or gaps.

Dispersers of megafaunal syndrome fruits — Megafaunal syndrome fruits are defined as fruits with diameters 40–100mm, having one to five large seeds, and fruits of diameter greater than 100mm having multiple small seeds (usually >100 seeds), characterized with distinct fruit diameter, mass, and seediness (Guimarães et al., 2008). They are fruits considered to be reliant on megafauna for dispersal and are expected to be vulnerable to extinction following the extinction and decline of megafauna (Doughty et al., 2016; Guimaràes, Galetti & Jordano, 2008). At present, elephants are expected to be able to disperse 'megafaunal syndrome' fruits more efficiently than smaller animals.

In the collection, 22% (36 out of 164) of the plant species were larger than 40mm. Only the *Artocarpus* species have the potential of reaching diameters of 100mm. (*Artocarpus lanceifolius*, 116mm, 13 seeds; *Artocarpus rigidus,* 94mm, 37 seeds; and *Artocarpus elasticus*, 96.5 mm, 119 seeds). Excluding the *Artocarpus* spp., 12 plant species had five or fewer seeds, and 17 plant species had more than five seeds. These 17 plant species are thus out of the main spectrum of neotropical megafaunal syndrome fruits, as described by Guimarães et al. (2008). 14.4% of (177 out of 1229) the total seed dispersal interactions involved fruits 40mm and larger. Of the 177 interactions, 49 (28%) belong to *Artocarpus* spp. With the inclusion of different seed dispersal methods, I found 22 animals capable of dispersing these species (11 animals swallowed seeds).

The Asian elephant dispersed 80.6 % (29 of 36) of the 'megafaunal syndrome' fruits. They represent 16% (29 out of 177 interactions) of the seed-dispersal interactions involving plant species with fruits larger than 4cm. Elephants swallowed fruits with seeds up to 46.9mm wide. Rats hoarded 52.8% (19 out of 36 plant species) of the 'megafaunal syndrome' fruits. They represent 11% (19 out of 177 interactions) of the seed-dispersal interactions involving plant species larger than 4cm. Rats hoarded seeds of sizes up to 46.9mm.

The rhinoceros are potential dispersers of megafaunal syndrome fruits but are have gone extinct from the Belum forest. With the decline of megafauna, megafaunal syndrome fruits with small seeds (<15mm) are likely safe from detrimental effects. Large fruits 40mm and greater with large seeds (15mm and greater) will likely suffer reduced overall fitness. They could be threatened with increasing aggregation, reduced geographic ranges, limited genetic variation, and increased among-population structuring (Seidler & Plotkin, 2006; Guimarães et al., 2008). With the loss of megafauna, rats and other rodents would thus be the remaining key dispersers for these plants.

Further Attributes Underlying the Belum Seed-dispersal Network: Guilds and Functionalities

Birds and the importance of hornbills – Except for the Great argus, all other birds were grouped within the same module. In this module, hornbills dispersed the greatest diversity of seeds and are important in helping to bond (highest z value amongst birds) and connect (highest c value amongst birds) modules. Capable of storing fruits in their gular pouch and oesophagus, hornbills provide a high-quality seed dispersal service by frequently transporting seeds to resting perches or roost sites, at medium to long distances (Kitamura, 2011; McConkey & Brockelman, 2011). In this study, hornbills dispersed 61 plant species. 62% (38 species) of seeds dispersed were carried and regurgitated. The fruit (mean 21±22mm, min. 6, max. 116) and seed sizes (mean 8±5mm, min.1, max.22) dispersed by hornbills were much larger than the average of fruit (mean 13±11) and seed (mean 6±3) dispersed by birds. From PCA, hornbills were highly correlated to the functionally important gibbons (1.0) and the Asian elephant (0.8).

The highly frugivorous Asian fairy-bluebird and barbets were examples of other birds that were important for keeping the avian module intact, with high z values in the network. Birds less important as dispersers were less frugivorous birds. Doves, green pigeons, parrots are seed predators (Dowsett-Lemaire, 1988; Bollen et al., 2004; Walker, 2007), ioras are insectivorous birds that are selective in the fruits they consumed (Kamruzzaman & Asmat, 2008), while nuthatches and jays are highly insectivorous birds that are also known to cache seeds (Bossema, 1979; Thibault et al., 2006).

I separated the Asian fairy-bluebird (0.075kg) from other leafbirds (0.03kg) to detect differences due to their body size. In the tropical semi-evergreen forest of Arunachal Pradesh, North-east India, the observations of birds that were also represented in the network provided a useful cross-reference. The lineated barbets were recorded feeding on the highest number of plant species (29), more than the white-throated bulbul (26), and hornbills (max. 12 spp.). Even so, the Great hornbill and Wreathed hornbill swallowed (around 90%) and removed a high number of fruits (up to 32mm). Hill Mynah and the Oriental pied hornbill also swallowed a large proportion of fruits (80%) but with a low removal rate. Smaller birds swallowed fruits of different sizes: barbets (max. 25mm), green pigeons (max. 19mm), the Asian fairy-bluebird (max. 16mm), and bulbuls (max. 12mm). However, the Lineated barbet swallowed (25%) and removed a lower proportion of fruits compared to the larger birds (Naniwadekar, 2019). Fruits sampled in Naniwadekar's study comprised of dehiscent fruit that could increase the mean measurement of the actual size swallowed by the birds. In this study, I limited the size of dispersed dehiscent fruits to seed sizes, rather than fruit sizes swallowed.

The seed dispersal importance of medium and smaller-sized birds is less studied and recognized compared to the hornbills in the South-east Asian landscape. Due to the multiple ways in which birds handle and disperse seeds, i.e., swallowing and defecating seeds, storing in the esophagus and gular pouch, and regurgitating seeds, processing seeds in the stomach and vomiting pellets, I found it a challenge to assign their seed treatment accurately (explained in Assignment of Seed Dispersal Interactions: Birds). In the Belum network, most bird taxa were represented by multiple species. Similar to other taxa with numerous species, I would expect differences in network metrics to vary between these birds, although they may still be differentiated from most mammal species in the PCA biplots. The effectiveness of seed dispersal by birds could also differ as a result of the social and feeding behaviour rather than a limitation of fruit traits. For example, flock feeding may disperse seeds at high density in clumps or scatter seeds in low density (Chavez-Ramirez & Slack, 1994), in which scattered seeds have a higher chance of germination success (Howe, 1989; Corlett, 1998; Albert et al., 2013). These are aspects not considered within the network.

If the differences in interaction strength and effective dispersal by different birds are discerned, separate modules could emerge within the bird community. The modules could also be temporal and fluctuate according to the fruiting period of different plant species (Silva et al., 2016). More specialised relationships between birds and the species they help to disperse might be observed (Sarmento et al., 2014). Few plants efficiently dispersed by specific bird species will be more tightly linked to their dispersers. A large proportion of plants less efficiently dispersed are likely to become more peripheral (reflected with longer distance in Fig. 4.06). It is also noteworthy that I had not exclude shrubs, epiphytic, higher altitude, and small-statured plants in the collection, several of which are dependent on birds for dispersal (e.g., Reid, 1989; Englund, 1993; Garcia et al., 2010). If these plants were included, birds would likely have shown more importance in the network. Birds are likely to be differentiated into more modules, as found in available network studies on birds (Scheleuning et al., 2010; Sarmento et al., 2014). More work is necessary to fill the knowledge and data gaps of seed dispersal by birds in the Sundaic rainforest. This network, nonetheless, provided a good baseline for the relative roles of different animal taxa (including other mammals) in the seed dispersal community.

Langurs in an individual module — Langurs (three species represented in the group) emerged as the sole seed disperser representing module two. Its grouping could be due to its adverse gut effects on seeds ingested (Bai et al., 2019), resulting in a much lower number of seeds dispersed as compared to other primates. Unlike the monogastric primates that frequently consume acidic, succulent fruits, langurs preferred leaves, dry fruit, and seeds (Leighton & Leighton, 1983; Ungur, 1993; Adhikaree & Shrestha, 2011). Of the three species in Belum, *Presbytis cristata* is mainly folivorous, while *Presbytis obscura* and *Presbytis melalophos* feed on leaves, fruits, and seeds (Curtin, 1980).

In this study, langurs fed on 141 species of both dry and fleshy fruited species, with amongst the highest record for non-mutualistic interactions (74 species with the seeds predated, 40 with seeds dropped) after squirrels (seeds hoarded: 15, destroyed: 107, seeds dropped: 26). 23 plant genera had supporting references of fruit consumption, while only five plant genera confirmed seed predation. Most studies did not provide information on whether fruits or seeds were eaten unripe. Leaf monkeys can detoxify some fruits such as the strychnine-containing

Strychnos species (also eaten by pheasants), and the cyanide-containing *Elateriospermum tapos* (eaten unripe by leaf monkeys) (Raemaekers et al., 1980).

The eight species associated with langurs under the same module were all small-seeded fleshy fruits (mean±SD: 6±2 mm; min. 2mm, max. 9mm). The potential of colobine monkeys (langurs in this study) as seed dispersers is under-explored. Still, there have been a few recent studies indicating they disperse a small number of plant species (e.g. Sethi & Howe, 2012; Bai et al., 2019). As observed of golden snub-nosed monkeys (*Rhinopithecus roxellana*), seed destruction varied among plant species and is not entirely determined by seed sizes (Bai et al., 2019). The role of langurs appears less critical in terms of the number of species dispersed, but their extinction might result in the loss of a phylogenetically outstanding group, and functionalities (e.g., mediating Dipterocarps recruitment as pre-dispersal seed predators; Sun et al., 2007) not explored in this study.

Rats and other rodents — At least fifty species of rodents exist in Peninsular Malaysia (Azma, 2011), and at least 11—20 rat species, excluding the bamboo rats, can be found in Belum (Table 4.02). In this study, multiple rat species were assigned under a single "rat" group and, hence, the network metrics for this group encompassed the functions of numerous species. If individual rat species are represented in the network, there might be a reduction in an individual's species strength. In PCA, individual species may spread out around the biplots, lying between 'largest seed dispersed' and 'PDI' (specialism). While some studies confirm the caching of large seeds by rodents (Xiao et al., 2004, 2005), the removal and caching (whether scatter-hoarding or larder-hoarding) of seeds can be variable between rodents sizes (Li & Zhang, 2003; Yi et al., 2014). Further, some rat species are likely generalists and some specialists. The effects of their generalism could mirror what was found in a spore-dispersal network. Spore-specialists generally dispersed a more diverse community of spores. When the abundance of generalist dispersers peaked, however, their importance surpassed that of specialists (Stephen & Towe, 2020).

Amongst rats, the long-tailed giant rat is a large-bodied rodent and might hoard more seeds than other rats. Previous studies have shown the long-tailed giant rat and the spiny rat (*Maxomys* spp.) scatter-hoard seeds in the Pasoh reserve, Malaysia. Scatter-hoarding of seeds in shallow caches results in lower recovery success as compared to larder-hoarding of seeds in deeper caches (Smith & Reichman, 1984; Vander Wall, 1990; Jansen & Forget, 2001). Although the caches were quickly retrieved within a day (78.7%), the long-tailed giant rat removed seeds up to 29m away from the feeding platform (range 0.4–29.4m; mean 16.1m) (Yasuda et al., 2000).

Porcupines were the second most important disperser in module four, as reflected by their species strength and *z* value. The Malayan Porcupine (*Hystrix brachyura)*, Asiatic brush-tailed porcupine (*Atherurus macrourus*), and long-tailed porcupine (*Trichys fasciulata*) are found in the Belum forest. From the camera trap observations of the Malayan porcupine feeding on fruits of *Parinari cf. oblongifolia* (Chrysobalanaceae) (Appendix Table A4.1), I noticed on one occasion that the Malayan porcupine had not immediately consumed the seed it found. Instead, it had removed the pulp of the stone fruit with a hard seed, left it on the spot, and continued feeding on the seed the night after. The Malayan porcupine was also observed removing a pod of *Callerya* species (Fabaceae) (Appendix Table A4.1). The feeding behaviour of porcupines could have led to potential scatter-hoarding of seeds or the promotion of secondary dispersal. Further studies may explore the hoarding behaviour of porcupines in the Sundaic rainforests. The likelihood of seed caching alters according to fruit traits such as seed coat thickness (thick-coated seeds were removed slower), germinability of seeds (early germinating species were eaten instantly), caloric level (high caloric seeds are likely to be larder-hoarded) (Yi et al., 2014). These fruit traits can be investigated along with the seed dispersal behaviour of porcupines or other seed hoarders.

In general, small-bodied animals such as rodents are more resilient to habitat degradation than massive animals (Ripple et al., 2016). If most large animals are extinct, rats (as a group) could increase in species strength within the network. On the other hand, reduced frugivory by other species could also result in a higher abundance of fruits available for rodents during the lean periods (Forget et al., 2002), thus reducing their need for hoarding, and compromising effective seed dispersal. The effects of hoarding in defaunated systems tied with fruit availability are difficult to predict. Further studies are needed in a defaunated dipterocarp forest to determine if the effects are positive or negative.

Large Bodied Seed Dispersers

Vidal et al. (2013) had proposed the possibility of large-bodied vertebrates, often generalists with wider gapes, serving as hubs in seed dispersal networks. This is supported by the Brazilian Pantanal network study where Donatti et al. (2011) found large vertebrate seed-dispersers such as the feral pig and the lowland tapir (*Tapirus terrestris*) served as hubs. In the Belum network, I found important animals include a wide range of sizes — animals with the highest species strength were gibbons, the Asian elephant, and rats (represented by multiple species). Despite the variation, animals of relatively high importance do include dispersers that were relatively large within the community or its taxonomic group, including dispersers such as binturong, civets, Malayan sun bear, wild boar, and hornbills that served different roles.

Overall, the capacity of 'large vertebrates' in seed dispersal is constrained by ruminants' tendency to masticate seeds in their oral cavity (Chen & Moles, 2015). As such, only protected hard stony seeds that are usually drupe fruits have the potential to be regurgitated and dispersed by ruminants (Chen et al., 2001; Prasad et al., 2006). I found seeds defecated by large ungulates such as the sambar deer and gaur (delimited in this study as 8.2mm and 10.6mm respectively) were small. On one occasion, I spotted large seeds of *Willughbeia cf. flavescens* (Apocynaceae; seed size: 20mm) fragmented in a ruminant dung pile along the transect. Although the ruminants regurgitate large seeds, few species (sambar deer: 16 and gaur: 2) were recorded in comparison to seeds spat by other vertebrates such as the Malayan flying fox and macaques. This could be partly contributed by the lack of observations by the Orang Asli and published records.

The role of the Malayan tapir was not prominent in this network. Their role in seed dispersal is less than elephants because they often reduce seed viability and disperse seeds over shorter distances than elephants (Campos-Arceiz et al., 2011). Tapirs can consume fruits up to 116mm (fruit width). However, seeds dispersed were limited to 26mm (Sridhara et al., 2016). Additionally, they commonly disperse seeds such as fig and palm species in latrines that may suffer reduced rates of seed predation by rodents, as found in Amazonian tapirs (Fragoso & Huffman, 2000; Quiroga-Castro & Roldan, 2001).

Siamang (*Symphalangus syndactylus*), the largest Hylobatidae was included in the LEK interviews but subsequently excluded from the network due to the difficulty in the identification of seed treatments. Available siamang studies were mainly diet rather than seed dispersal oriented. Siamang is currently endangered (IUCN), and its population is diminished as compared to the past in Belum (general statements observations by Orang Asli). Being canopy-dwellers left with remnant territories in BTFC, their functionalities, and the LEK tied with it is vulnerable (Cámara-Leret et al., 2019). Siamang is more commonly recognized as folivorous, feeding mostly on leaves. Elder (2009), however, found that Siamang might spend more than 50% of their feeding time on fruits, of which nearly 30% are targeted on figs. They are the largest gibbon and have the potential to access even larger seeds than the gibbon species recorded in this study.

Amongst the important large-bodied seed dispersers, both the Malayan sun bear and binturong are listed by IUCN as vulnerable species. Grouped under arboreal mammals in this study, the Malayan sun bear is a semi-arboreal mammal that climbs trees 25% of the time for fruit feeding, favouring figs, and higher caloric fruits of mast species (Fredriksson et al., 2006). Although the effectiveness of the Malayan sun bear in seed dispersal is variable, seedling survivorship of seeds defecated by the Malayan sun bear can be as high as 53% (McConkey & Galetti, 1999). In the Belum network, their importance in maintaining network nestedness is moderate-high, falling behind binturong in the *z* value. As represented in the network by civets and the Malayan sun bear, carnivorous animals can be important seed dispersers. I did not include seed dispersal interactions by the Yellow-throated marten (*Martes flavidula*). In Japan, the Japanese marten (*Martes melampus*) were found to disperse 11 to 28 plant species (Otani, 2002; Tsuji et al., 2011). The Yellow-throated marten may be included in future seed dispersal studies.

Binturong is the largest civet native to South and Southeast Asia. In the network, they appeared less important than gibbons, the Asian elephant, and rats, but they have species strength above other animals in the system. Binturong has a broad habitat range, with a mean daily travel distance of 688±667 m (mean±SD) (Grassman et al., 2005), and could serve as long-distance seed dispersers for the plants they consume. Despite its widespread distribution from South to Southeast Asia, there are limited studies of seed dispersal by binturong. I hence referenced binturong's seed dispersal from civets. As a larger sized Viverridae (family), I assumed they have the potential to disperse seeds from similar plant genera. In the Bornean rainforest, however, radio-collared binturong revealed that they are highly dependent on figs for food (Nakabayashi & Ahmad, 2018). Their habit of defecating faeces in microsites in the canopy was also found to be highly reliable for the germination of hemi-epiphytic figs as compared to the Muller's gibbons (*Hylobates muelleri*) and helmeted hornbill (Nakabayashi et al., 2019).

Ficus, the Supergeneralist in the Network

This study was not intended to describe the roles of plants in the network in detail. In the Belum network, no animal emerged as a super-generalist. Super-generalists are species that serve as both hubs and connectors (Donatti et al., 2011; Dormann, 2014). Of all plant species, results revealed three *Ficus* spp. (Moraceae) and *Microcos cf. globulifera* (Tiliaceae) as super-generalists. Four *Ficus* spp. and *Aidia densifolia* (Rubiaceae) were found to be the only plants that had positive pulling effects (network metric not presented in results) on the animals they interacted with. Existing studies showed that multiple species are highly dependent on figs — including the binturong (Nakabayashi & Ahmad, 2018), birds such as barbets, bulbuls, and hornbills (Brockelman, 1982; Kinnaird et al., 1996; Sanitjan & Chen, 2009; Caughlin et al., 2012), the Malayan flying fox (Chen et al., 2017), bats (Shanahan et al., 2001), and gibbons (Raemaekers, 1978; Palombit, 1997).

A review by Shanahan et al. (2001) of records from over 75 countries collected 260 Ficus species (30% of described species) that were consumed by a few reptiles, fishes, 1274 bird and mammal species from 523 genera and 92 families. Observing pigeons, parrots, hornbills, and passerines for 20 months in Sulawesi, Walker (2007) recorded 120 species being consumed by an assemblage of birds. The birds depended on fruits for 44 to 100% of their diets, of which figs comprised 57% of all observations. Figs were important fruits to the birds even in periods when alternative fruits were not scarce.

Ficus are identified as keystone plants as they provide important food resources to a large community of animals throughout the year, including the period of food scarcity (Terborgh, 1986). Recording frugivory and seed dispersal interactions during this period may not capture the diversity of a frugivore's diet, and could lead to a biased conclusion of a fig-dominated diet for some frugivores. Being such important plant species, it is worth further investigating the dispersal patterns of *Ficus* relative to other plant species in the community.

More plants than animals emerge as hubs and connectors in the networks. Other important plants include network hubs *Bouea macrophylla* (Anacardiaceae), *Garcinia parvifolia* (Ebenaceae), and all *Artocarpus* species, and network connectors *Desmos* sp. 1 (Annonaceae), *Prunus* sp. 4 (Rosaceae), and Burseraceae sp. 1 (Burseraceae). I presented only brief perspectives on plants in this study. A separate paper is required to consider the role of plants in the seed dispersal network.

Defaunation and the Belum Landscape

The seed dispersal network showed high robustness to random extinction (animal: 0.82, plants: 0.96). The network, however, is more fragile than this reflects because a high number of highly-linked and important dispersers are currently threatened by anthropogenic activities. The removal of highly linked species such as these may lead to resource depletion, creating cascading effects of co-extinctions (Rezende et al., 2007). Amongst important dispersers, the helmeted hornbill is critically endangered. Gibbons, the Asian elephant, the white-crowned hornbill, and the wrinkled hornbill are endangered. Binturong, the Malayan sun bear, and the pig-tailed macaque (*Macaca nemestrina*) are vulnerable. By progressively removing the highest connected species, I found rapid secondary extinction of (the functional dispersal of) plants. While plants are usually resilient, the loss of pivotal species resulted in a cascading effect on the plant community. Losing plants from the network also results in the rapid extinction of animals. This may be more appropriately interpreted as the loss of functionalities than species extinction as most animals in the community are not true frugivores and may depend on an alternative diet for survival.

The seed dispersal process is one of the most threatened processes due to human disturbance (Neuschulz et al., 2016). Defaunation of species is often non-random, and functionalities are often degraded before a species is vulnerable (Hooper et al., 2005; Dirzo et al., 2014). At present, the Belum forest faces high hunting pressure and poaching activities (Loke et al., 2020). Most of Belum's lowlands that are important for wildlife were flooded following the development of the 180km^2 Temenggor Dam in 1977, and its floristic composition of lowland forest species was greatly diminished as a result (Rayan & Linkie, 2015). The current altitude of the sampled transects ranged from elevations between 280–430m. In the forest, I found several species (e.g., *Dillenia indica*) important for large mammals restricted to lower altitude patches near lake fringes and some species as a single individual tree (e.g., *Parinari cf. oblongifolia*). The transects were spread over a relatively wide area across the RBSP, enough to capture trees of different dispersal syndromes (gravity, gyration, wind, animal-dispersed) except for ballistic dispersal when trees were highly clumped and the clumps are far from one another (refer dispersal pattern from Seidler & Plotkin, 2006). Thus, the extent to which important plant species and interactions have been lost is unknown, but the seed dispersal functions of large terrestrial mammals are likely compromised.

The most effective and important seed disperser in the network, the gibbons, are hunted heavily (Loke et al., 2020). Primates communicate using different calls. In tropical forests, long-distance calls by primates in the morning and intermediate distances in the evenings are distinct (Seyfarth, 1987). Gibbons use close-range "hoo" to communicate with one another (Clarke et al., 2015). The duets sung almost daily by mated females to defend their territories and by males to repel other males (Cowlishaw, 1992) are conspicuous, and enable us to detect gibbons in the forest. During the sampling period, however, such vocalizations were not common near the sampling sites. Instead, elephant signs appeared more common as their dung piles can be found along trails. Gibbons are the preferred food of local indigenous people (Loke et al., 2019). However, according to the Protection of Wildlife Act, 1972 (Or & Leong, 2011), only ten species were allowed for hunting by the Orang Asli — including the wild boar, sambar deer, lesser mouse deer, pig-tailed macaque, silvered leaf-monkey (*Trachypithecus cristatus*), dusky leaf-monkey, Malayan porcupine, brush-tailed porcupine, white-breasted water-hen (*Amaurornis phoenicurus*) and emerald dove (*Chalcophaps indica*). The hunting of gibbons by local indigenous people is thus constrained. Nevertheless, the presence of illegal poachers is common in BTFC. I found animal traps, words in a foreign language carved into trees, had camera traps stolen and had many destroyed tree tags in the forest. A defaunation shadow occurs when the demand for a species leads to adverse effects on its population. Over-exploitation could collapse the mutualistic interactions and ecological function of the hunted species (Laurance et al., 2012; Costa-Pereira & Galetti, 2015; et al., 2018). I speculate that with the current status of gibbons, the role of the Asian elephant in keeping the resilience of the seed dispersal functions is likely more critical in areas where gibbons are absent.

Fruits in the network had a median diameter of 19mm (mean 27±22 mm, min. 3mm, max. 116mm). Fruits of these sizes are relatively small to be appealing to elephants. Yet, the Asian elephant was important for the dispersal of plants central to the network and fruits around this size. Around 40% of the fruits that can be dispersed by the Asian elephant were smaller than this fruit size. Video footage from the camera traps captured a group of elephants spending a long time under a fruiting *Bouea macrophylla* (Anacardiaceae) tree (fruit size 22.8mm). The complementary importance of the Asian elephant to gibbons could reflect the scarcity of large-fruited species fruiting in the forest. While elephants specialise on large-fruited species as shown in PCA 2, they may feed opportunistically on other smaller-sized fruits (PCA 1) that are central to the network when the preferred food sources are scarce (Fleming, 1986). This optimal foraging strategy enables the maximization of net energy at low cost (MacArthur & Pianka, 1966). During the sampling period, only a few large species such as the *Xylopia* sp. 1 (Annonaceae), and *callophyllum macrocarpum* (Calophyllaceae) had a massive crop when fruiting. Studies specific to the phenology of large-fruited species could determine fruit availability for larger frugivores and how effectively large-fruited species are dispersed.

In Belum, the artificial dam has created a landscape where huge water bodies separate the once continuous forest that is highly utilised by wildlife. Animals are not able to cross the lake easily as they would have been able to for streams or rivers. Thus, in the Belum forest, seed dispersal and pollination functions are fragmented by the lake. Only animals that have broad home ranges and high adaptability to disturbance or human presence, such as the Asian elephant, hornbills, and bats, can facilitate dispersal between the eastern and western sides of the forest. Being the most highly functional flying species in the network, hornbills, in particular, help facilitate the connectivity of the landscapes (Mueller et al., 2014). Bats dispersed seeds up to 32 mm in the collected samples. From interviews with Orang Asli, however, sightings of the Malayan flying fox (the largest bats) are low. The Malayan flying fox has low ecological redundancy, but their functionalities cease before they become rare because seed dispersal is dependent on high enough numbers to induce aggressive interactions (McConkey & Drake, 2015). Little information is available for Malayan flying fox in the BTFC. There is an urgent need to survey, conserve, or recover its population along with the restoration of suitable habitats for the flying foxes in BTFC. Efforts to improve the connectivity between both sides of the forests can be explored.

This network provided a community perspective of the seed dispersal process in a highly diverse dipterocarp rainforest. It enables us to understand the roles of medium-sized and large vertebrates and animals important to the seed dispersal community. While networks allow us to understand the broader seed dispersal patterns, other mechanistic studies are required for a fuller picture of seed dispersal dynamics. Studies relating to temporal dynamics, animal abundance and activity patterns (Wright et al., 2000; DiVittorio et al., 2007; Côrtes & Uriarte, 2013), probability of caching (Jansen & Forget 2001), variation in seed production and the effects of masting (Jordano et al., 1998; Wright et al., 1999), post-dispersal (Howe, 1993), germinability and germination time of seeds (Broschat & Donselman, 1987; Torres et al., 2020; Thapliyal & Phartyal, 2005) are required. In areas such as Belum where rapid defaunation is taking place, important functions could be lost before the knowledge gaps are filled.

Local Ecological Knowledge

The use of LEK was essential to this study and to achieve the objective of describing the seed dispersal network. When I gathered information from six villages, I received negative feedback that the subsistence of LEK knowledge is threatened as the younger generation is introduced into the mainstream lifestyle. Progressively more people are detached from the forest as they take on non-forest related jobs to sustain their livelihood. It was a challenge to find candidates who possess plant-animal interaction knowledge, although a large proportion of people were familiar with plant and animal names. It was particularly challenging to find participants who were familiar with the plant-animal interactions of smaller-bodied birds. Similar to the Neotropics, LEK erodes quickly with cultural diffusion (Cámara-Leret et al., 2019). I found LEK of an animal vanished rapidly following its extinction, due to reduced observations, animal signs to associate the environment with, and no written records. Concrete records of Sumatran rhinoceros spotted in Belum dated back to 2007 (Magintan et al., 2010). At present, I was unable to gather useful frugivory information regarding what the extinct rhinoceros consumed. An old participant, age 81 (in 2018), mentioned that the picture was the first time he saw what the rhinoceros looked like, while younger participants (aged around 30–50) mentioned they had seen signs of rhinoceros before.

As described under methods, the seed handling by gibbons was likely mixed with macaques' feeding in the responses. I was able to improve the dataset with a multi-disciplinary approach. Due to an existing erosion of LEK, it would be unsafe to depend entirely on LEK to describe the data. Neither do I suggest relying on one or two individuals for the LEK as the error could be high. While the design had its limitations, I saw the need to design interviews that catered to the indigenous people's way of thought. For example, it would have been more useful to have complete herbariums or be in the forest with the fruiting tree for the interviews. Resources were limited, and hence a pictorial reference served as a useful alternative.

This community approach study is only possible with the utilization of LEK, and I recognize the importance of LEK to biological sciences. Mitigations are needed to prevent the decline of both LEK and natural sciences in Malaysia over the next 20 years. I recognize the most urgent task for biological conservation concerning the LEK as 1) Ensuring that the knowledge and skills continue to be passed on to the younger generations. 2) Formalizing a para-taxonomy oriented education that could incorporate the indigenous people's way of learning while providing them with highly credited certifications. 3) Recording accurate information concerning plant-animal interactions and, at the same time, 4) ensuring that the indigenous people receive equitable sharing of benefits and stable income from the use of LEK. 5) I need to be careful that in the process of documenting LEK (including information added to the DNA library), local indigenous people will not be eventually excluded from long-term jobs when the information is readily made available. Actions for preserving LEK need to be incorporated in more formal ways that would provide them the security of an income with their skills.

Early in the 1970s, Bolton (1972) described and classified Orang Asli as deep jungle nomads, deep jungle settlers, and jungle fringers. Deep jungle nomads survive mainly on jungle roots, supplemented by hunting and fishing. Deep jungle settlers practice slash-and-burn shifting cultivation, hunt with blowpipes and traps, and occasionally collect wild vegetables and fruits. Jungle fringers live in settled villages outside the jungle. This group of Orang Asli may practice shifting cultivation, but at the same time rely on rubber plantations and rearing of livestock for their needs. At present, many of these practices are still carried out but mixed with modern living. I encourage conscious efforts to preserve the original cultures and heritage of indigenous lives.

CONCLUSION

The Belum seed dispersal network was modular, nested, connected, and generalised. These combined characteristics confer network resilience to species and functional extinction. Resilience also results from the presence of multiple complementary seed-dispersal relationships, i.e., gibbon-elephant, and elephant-rats, amongst the dominant seed dispersers from different forest strata. The gibbons were the most effective and dominant seed dispersers for plant species central to the network. Rats were important for the hoarding of large-seeded species. The Asian elephants emerged as important functional-generalists, spreading their influence across both central and large-seeded species. Network nestedness attributed to high generalism and was the pivotal structure contributing to the robustness of the network to random extinctions. Such processes could result in generalised interactions with high productivity and diversity. Other animals of relatively high importance include highly generalised seed dispersers such as civets, binturong, hornbills, the Malayan sun bear, and macaques, as well as moderately generalised animals such as langurs, the Asian fairy-bluebird, barbets and wild boar. Civets, hornbills, barbets, and rats were large taxonomical groups that comprised multiple species. Hence, the importance of less frugivorous species within the taxa could be amplified.

The Belum seed dispersal network is more fragile than reflected by the results as the robustness of the system was based on random extinctions. At present, the Belum forest has been subjected to high hunting pressure, and most of the highly generalised important species are either endangered or vulnerable. Simulation of the progressive extinction of the most connected species showed a rapid coextinction of plant species as compared to random extinctions and the loss of rare interactions. Defaunation thus created a cascading effect on the seed dispersal function and fitness of plants. At present, an erosion of LEK is apparent, and urgent efforts are required to prevent the collapse of this knowledge. Such a failure could jeopardize both the heritage of Orang Asli as well as biological sciences that are highly dependent on them for their knowledge. A community-oriented study is crucial, especially for megafauna such as elephants. This study would not be possible in the challenging and highly diverse Sundaic rainforest without the inclusion of LEK.

APPENDIX

Table A4.1 Sampled plant species in the seed-dispersal network. Plant ID is equivalent to the numbers found in other figures in this chapter.

Plant ID	Family	Plant	Seed Number	Fruit Weight	Fruit Width	Seed Width
1	Combretaceae	*Combretum* sp. 1	1	0.3	2.8	2.3
2	Sapindaceae	*Allophylus* sp. 1	1	0.1	5.5	0.7
3	Annonaceae	*Goniothalamus* sp. 2	2	0.2	5.7	3.9
4	unknown	*Perpir**	1	0.4	5.8	5.0
5	Annonaceae	*Huberantha cf. rumphii*	1	0.3	6.3	5.5
6	Rubiaceae	*Aidia densiflora*	27	0.3	7.0	1.2
7	Annonaceae	*Desmos* sp. 1	4	0.9	7.3	5.8
8	Annonaceae	*Goniothalamus* sp. 1	2	0.3	7.4	4.8
9	Dipterocarpaceae	*Shorea* sp. 2	1	0.7	7.6	6.6
10	Dipterocarpaceae	*Shorea* sp. 1	1	0.5	7.9	6.8
11	Dipterocarpaceae	*Shorea* sp. 3	1	0.7	7.9	6.3
12	Moraceae	*Ficus* sp. 4	18	0.3	7.9	0.8
13	Rhamnaceae	*Ventilago maderaspatana*	1	0.9	8.1	6.5
14	Anacardiaceae	*Gluta wallichii*	1	1.2	8.3	6.7
15	Ulmaceae	*Gironniera* sp. 1	1	0.3	8.4	4.8
16	Dipterocarpaceae	*Shorea* sp. 4	1	0.9	8.6	7.6
17	unknown	*Cenos**	1	0.4	8.6	7.0
18	Moraceae	*Ficus* sp. 3	70	0.4	8.8	0.7
19	unknown	*Akar Kacau**	1	0.9	9.0	6.2
20	unknown	*Nyapang**	1	0.7	9.0	6.7
21	Tiliaceae	*Microcos laurifolia*	3	0.5	9.2	3.7
22	Rhamnaceae	*Ziziphus* sp. 1	1	0.6	9.3	6.9
23	Anacardiaceae	*Pentaspadon velutinus*	1	0.2	9.5	8.0
24	Trigoneaceae	*Trigoniastrum hypoleucum*	1	0.2	9.5	4.2
25	Gnetaceae	*Gnetum* sp. 3	1	0.9	9.6	8.5
26	Staphyleaceae	*Turpinia* sp. 1	3	0.5	10.1	4.0
27	unknown	*Khel**	1	1.3	10.2	6.2
28	unknown	*Tahbit**	1	0.7	10.4	8.1
29	Rosaceae	*Prunus* sp. 1	1	0.3	10.4	4.0
30	Myrtaceae	*Syzygium* sp. 1	1	1.0	10.5	5.8
31	Annonaceae	*Polyalthia* sp. 1	1	1.0	10.6	5.8
32	Rubiaceae	*Psydrax* sp. 1	1	1.4	10.6	6.0
33	Meliaceae	*Aglaia* sp. 1	1	1.0	10.7	8.1
34	Rubiaceae	*Rubiaceae sp. 2*	1	0.8	10.8	6.5
35	unknown	*Akar Bod**	1	0.8	10.8	9.3
36	Ebenaceae	*Diospyros confertiflora*	1	1.3	10.8	7.4

(continued) Table A4.1 Sampled plant species in the seed-dispersal network. Plant ID is equivalent to the numbers found in other figures in this chapter.

Plant ID	Family	Plant	Seed Number	Fruit Weight	Fruit Width	Seed Width
37	Myrtaceae	*Syzygium* sp. 2	1	1.2	10.8	8.2
38	unknown	*Saweh**	1	0.6	11.2	6.2
39	Rubiaceae	*Aidia* sp.1	4	1.1	11.3	4.3
40	Lauraceae	*Cinnamomum* sp. 3	1	4.1	11.3	8.8
41	Lauraceae	*Cinnamomum* sp. 1	1	2.0	11.3	8.8
42	Moraceae	*Ficus* sp. 2	100	1.0	11.4	0.8
43	Euphorbiaceae	*Mallotus* sp. 1	3	0.6	11.5	4.2
44	Euphorbiaceae	*Mallotus* sp. 2	3	0.6	11.5	4.2
45	Elaeocarpaceae	*Elaeocarpus* sp. 1	1	2.3	11.7	8.0
46	Euphorbiaceae	*Macaranga tanarius*	2	0.7	11.8	4.4
47	Annonaceae	*Polyalthia* sp. 2	1	1.6	11.9	10.4
48	Moraceae	*Ficus* sp. 1	327	1.2	12.0	0.8
49	Dipterocarpaceae	*Dipterocarpus* sp. 1	1	2.6	12.1	9.4
50	Violaceae	*Rinorea anguifera*	6	1.5	12.2	4.3
51	Euphorbiaceae	*Macaranga* sp. 1	3	0.8	12.4	4.7
52	Annonaceae	*Uvaria* sp. 1	9	5.6	12.5	8.1
53	Flacourtiaceae	*Flacourtia* sp. 1	2	2.3	13.2	6.4
54	Rosaceae	*Prunus* sp. 4	1	1.2	13.2	7.1
55	Ebenaceae	*Diospyros* sp. 3	3	1.6	13.3	5.6
56	Flacourtiaceae	*Flacourtia* sp. 2	2	1.4	13.5	7.6
57	Burseraceae	*canarium* sp. 1	1	1.7	13.6	7.7
58	Sterculiaceae	*Heritiera* sp. 1	5	4.1	13.6	10.0
59	Gnetaceae	*Gnetum* sp. 2	1	2.5	13.7	10.5
60	Annonaceae	*Polyalthia* sp. 3	1	2.0	13.7	9.8
61	Gnetaceae	*Gnetum* sp. 1	1	2.7	14.0	8.7
62	unknown	*Selamak**	2	1.1	14.1	4.5
63	Burseraceae	*Burseraceae* sp. 1	1	1.3	14.4	8.6
64	Rosaceae	*Prunus* sp. 2	1	2.4	14.4	10.8
65	Myrtaceae	*Eugenia* sp. 1	1	0.8	14.5	12.3
66	Fabaceae	*Dialium* sp. 1	1	1.2	14.8	4.3
67	Tiliaceae	*Microcos cf. globulifera*	1	2.0	15.0	4.3
68	unknown	*Suwong**	2	2.2	15.4	6.7
69	Sapindaceae	*Pometia pinnata*	1	2.8	15.5	8.8
70	Sapindaceae	*Dimocarpus* sp. 1	NA	3.1	15.8	12.6
71	Euphorbiaceae	*Hancea* sp. 1	2	1.3	16.1	5.0
72	Magnoliaceae	*Magnolia* sp. 1	1	0.9	16.5	12.4
73	Annonaceae	*Alseodaphne* sp. 1	1	5.3	16.8	10.6
74	Fagaceae	*Lithocarpus* sp. 1	1	2.6	16.8	9.7
75	Ebenaceae	*Garcinia Parvifolia*	4	2.9	17.1	5.4

(continued) Table A4.1 Sampled plant species in the seed-dispersal network. Plant ID is equivalent to the numbers found in other figures in this chapter.

Plant ID	**Family**	**Plant**	**Seed Number**	**Fruit Weight**	**Fruit Width**	**Seed Width**
76	Sapindaceae	*Xerospermum noronhianum*	1	4.1	17.3	12.2
77	Fagaceae	*Lithocarpus* sp. 5	1	2.1	17.4	11.9
78	Annonaceae	*Cyathocalyx* sp. 2	13	5.7	18.1	7.4
79	Fagaceae	*Lithocarpus* sp. 4	1	2.7	18.2	10.6
80	Fagaceae	*Lithocarpus* sp. 2	1	3.2	18.3	11.1
81	Fagaceae	*Lithocarpus* sp. 3	1	3.2	18.3	11.1
82	unknown	*Rangoid**	1	3.2	18.4	NA
83	unknown	*Gayak**	1	6.6	18.6	13.9
84	Fagaceae	*Castanopsis* sp. 2	1	4.0	18.9	10.5
85	Fagaceae	*Lithocarpus encleisacarpus*	1	2.7	19.0	13.0
86	Arecaceae	*Calamus* sp. 1	1	6.3	19.2	14.3
87	Lauraceae	*Cinnamomum* sp. 2	1	4.1	19.2	11.7
88	Ebenaceae	*Diospyros* sp. 1	7	4.5	19.3	6.4
89	unknown	*Gelimbok**	1	3.6	19.9	1.9
90	Fagaceae	*Quercus* sp. 1	1	3.7	20.2	13.5
91	unknown	*Mantun**	1	6.2	20.4	13.4
92	Rosaceae	*Prunus* sp. 3	1	4.1	20.4	13.2
93	unknown	*Akar Gepbrat**	1	6.4	20.8	11.9
94	unknown	*Pleng**	NA	6.4	21.2	20.0
95	Lauraceae	*Litsea* sp. 1	NA	6.7	21.7	14.6
96	Euphorbiaceae	*Neoscortechinia* sp. 1	1	11.9	22.5	16.9
97	Ebenaceae	*Diospyros* sp. 2	6	8.1	22.5	7.9
98	Rubiaceae	*Gardenia carinata*	500	10.2	22.7	2.5
99	Anacardiaceae	*Bouea macrophylla*	3	9.7	22.8	11.9
100	Annonaceae	*Uvaria* sp. 2	1	7.4	23.6	13.1
101	Ebenaceae	*Garcinia* sp. 3	2	9.6	23.9	10.9
102	Moraceae	*Ficus* sp. 5	500	8.7	24.3	1.1
103	Styracacea	*Styrax* sp. 1	1	9.1	24.8	14.2
104	Ebenaceae	*Diospyros* sp. 6	4	3.5	25.1	8.9
105	Fabaceae	*Swartzia* sp. 1	3	6.7	25.5	10.5
106	Dipterocarpaceae	*Vatica* sp. 1	1	8.6	26.2	12.3
107	Meliaceae	*Lansium* sp. 1	4	14.2	26.3	7.5
108	Burseraceae	*Triomma malaccensis*	3	5.1	26.4	6.8
109	Fabaceae	*Koompassia* sp. 1	1	3.2	28.1	7.4
110	Anacardiaceae	*Dracontomelon dao*	1	12.5	28.4	16.2
111	Anacardiaceae	*Spondias cf. pinnata*	1	16.0	28.4	24.7
112	Annonaceae	*Xylopia* sp. 1	5	15.5	28.5	11.3
113	Dipterocarpaceae	*Parashorea* sp. 1	1	12.3	29.1	5.8
114	Callophyllaceae	*Mesua cf. ferrea*	2	14.4	29.1	19.4

(continued) Table A4.1 Sampled plant species in the seed-dispersal network. Plant ID is equivalent to the numbers found in other figures in this chapter.

Plant ID	Family	Plant	Seed Number	Fruit Weight	Fruit Width	Seed Width
115	Dipterocarpaceae	*Dipterocarpus grandiflorus*	1	22.2	29.4	20.3
116	unknown	*Cengang**	NA	NA	30.1	NA
117	Passifloraceae	*Adenia macrophylla*	8	5.9	30.5	7.3
118	Annonaceae	*Stelechocarpus cauliflorus*	6	21.8	31.3	10.4
119	Fabaceae	*Koompassia malaccensis*	NA	1.3	31.3	NA
120	Rubiaceae	*Porterandia anisophylla*	NA	17.7	31.9	3.5
121	unknown	*Jerantok**	NA	NA	32.0	NA
122	Euphorbiaceae	*Paracroton pendulus*	3	22.8	32.0	11.5
123	unknown	*Akar Terikai**	2	18.2	32.4	15.3
124	Fagaceae	*Castanopsis* sp. 1	1	12.8	33.5	23.6
125	Sterculiaceae	*Sterculia* sp. 1	3	20.2	34.2	12.8
126	Myristicaceae	*Knema* sp. 1	1	24.2	34.3	16.2
127	Annonaceae	*Alphonsea* sp. 1	8	43.7	37.8	11.9
128	Olacaceae	*Scorodocarpus Borneensis*	1	37.7	39.2	38.0
129	Irvingiaceae	*Irvingia malayana*	1	43.4	40.2	28.2
130	Euphorbiaceae	*Elateriospermum tapos*	3	18.0	40.7	19.1
131	Annonaceae	*Platymitra* sp. 1	11	54.2	41.1	15.8
132	Myristicaceae	*Myristica* sp. 1	1	49.3	41.1	21.9
133	Chrysobalanaceae	*Atuna racemosa*	1	26.9	41.5	25.7
134	Fabaceae	*Sindora* sp. 1	2	14.0	41.8	15.5
135	Arecaceae	*Eugeissona* sp. 1	1	50.6	42.1	36.9
136	Chrysobalanaceae	*Parinari cf. oblongifolia*	1	74.9	42.5	46.9
137	Rutaceae	*Citrus halimii*	8	49.9	46.8	9.3
138	Sterculiaceae	*Sterculia cordata*	2	36.9	48.7	16.1
139	Annonaceae	*Mezzetia cf. macrocarpa*	2	NA	50.0	29.9
140	unknown	*Cindros Kedik**	10	44.1	50.0	9.0
141	Ebenaceae	*Garcinia* sp. 2	5	88.9	51.0	8.2
142	Dilleniaceae	*Dillenia reticulata*	24	76.0	52.5	3.6
143	Calophyllaceae	*Calophyllum macrocarpum*	1	118.4	55.0	31.5
144	Annonaceae	*Cyathocalyx* sp. 1	6	105.0	55.7	19.2
145	Fabaceae	*Callerya* sp. 1	1	143.6	56.2	41.7
146	Ebenaceae	*Diospyros* sp. 5	6	89.8	57.3	18.6
147	Ebenaceae	*Diospyros* sp. 7	2	102.5	58.5	27.5
148	unknown	Cabol Kedik*	9	99.0	58.6	12.1
149	Achariaceae	*Hydnocarpus* sp. 1	NA	NA	59.7	28.2
150	Loganiaceae	*Strychnos* sp. 1	47	94.8	60.0	10.7
151	Ebenaceae	*Diospyros* sp. 4	9	119.5	60.3	14.2
152	Annonaceae	*Monocarpia marginalis*	8	153.3	63.2	19.8
153	Eleocarpaceae	*Sloanea javanicaulek*	6	227.5	64.3	12.5

(continued) Table A4.1 Sampled plant species in the seed-dispersal network. Plant ID is equivalent to the numbers found in other figures in this chapter.

Plant ID	Family	Plant	Seed Number	Fruit Weight	Fruit Width	Seed Width
154	Meliaceae	*Meliaceae* sp. 1	3	151.9	65.2	24.9
155	Ebenaceae	*Garcinia cf. xanthochymus*	2	139.3	65.5	25.7
156	Fabaceae	*Fabaceae* sp. 1	7	118.6	70.1	26.8
157	Fabaceae	*Intsia palembanica*	5	129.5	80.2	24.9
158	Apocynaceae	*Willughbeia cf. flavescens*	19	400.1	82.7	19.9
159	unknown	*Simelyong**	NA	NA	85.0	26.4
160	Malvaceae	*Neesia* sp. 1	NA	158.9	89.6	NA
161	Rutaceae	*Citrus macroptera*	36	291.0	89.7	8.0
162	Moraceae	*Artocarpus rigidus*	37	279.5	94.4	9.9
163	Moraceae	*Artocarpus elasticus*	119	510.6	96.5	8.8
164	Moraceae	*Artocarpus lanceifolius*	13	740.3	115.7	10.6

Table A4.2 Network-level metrics of Belum (Sundaic, Indomalaya), Afrotropics and Neotropics (Dugger et al., 2018). H_2': Afrotropics is represented by 17 networks, neotropics is represented nu 48 networks.

	Belum	**Afrotropics**		**Neotropics**	
		median	25th to 75th percentile	median	25th to 75th percentile
Weighted NODP	26.3	40	20–60	30	12–53
Modularity	0.298	0.36	0.19–0.58	0.38	0.17–0.6
Interaction evenness	0.796	0.78	0.62–0.9	0.83	0.73–0.97
Specialization, H_2'	0.225	0.22	0.03–0.47	0.35	0.1–0.55

Table A4.3 Between group scores of the correlation matrix (arranged according to scores: high to low); in green (top 3), in yellow (top 10)

Animals	**PC 1**	**PC 2**	**PC 3**
Gibbons	5.2	-0.9	-0.2
Asian Elephant	3.0	2.0	-0.3
Binturong	2.4	-1.1	0.3
Civets	2.2	-1.4	-0.1
Malayan sun bear	1.4	-0.2	0.6
Rats	1.2	2.7	-0.1
Macaques	1.2	-0.2	0.5
Hornbills	0.9	-0.1	-0.3
Asian fairy-bluebird	0.7	-0.8	-0.3
Barbets	0.7	-1.0	-0.3
Langurs	0.4	-1.1	0.2
Sambar deer	0.1	-1.0	-0.2
Southern red muntjac	0.1	0.2	0.4
Hill Mynah	-0.1	-0.9	-0.1
Malayan flying fox	-0.1	0.8	0.0
Porcupines	-0.1	2.0	-0.9
Bats	-0.2	1.6	0.7
Leafbirds	-0.2	-0.6	0.2
Squirrels	-0.4	1.5	0.6
Malayan Tapir	-0.5	0.5	-0.6
Human	-0.5	2.0	-0.2
Wild boar	-0.6	-0.6	0.3
Parrots	-0.7	-0.7	-0.1
Bulbuls	-0.7	-0.4	-0.1
Green pigeons	-0.8	-0.7	-0.1
Great Argus	-0.8	-0.1	0.3
Gaur	-1.1	-0.2	-0.4
Ioras	-1.1	-0.5	0.0
Mousedeers	-1.4	0.0	0.3
Doves	-1.9	0.3	0.0
Jays	-2.0	0.0	-0.3
Flying squirrels	-2.1	-0.6	0.0
Colugo	-2.1	-0.7	0.2
Nuthatches	-2.2	0.1	-0.2

Table A4.4 Within group scores of the correlation matrix (arranged according to scores: high to low); in green (top 3), in yellow (top 10)

Animals	**PC 1**	**PC 2**	**PC 3**	**PC 4**
Gibbons	5.3	-0.2	-0.7	0.3
Asian elephant	2.7	2.4	-0.6	0.2
Binturong	2.5	-0.7	0.5	0.2
Civets	2.4	-1.0	0.7	-0.3
Malayan sun bear	1.4	0.0	0.8	0.4
Macaques	1.2	-0.1	0.4	0.5
Hornbills	0.9	0.1	0.0	-0.3
Rats	0.9	2.8	-1.0	0.6
Barbets	0.8	-0.9	0.1	-0.4
Asian fairy-bluebird	0.8	-0.7	0.0	-0.3
Langurs	0.6	-1.0	0.1	0.1
Sambar deer	0.3	-0.9	0.1	-0.4
Hill Mynah	0.1	-0.8	0.0	-0.2
Southern red muntjac	0.0	0.3	0.7	0.2
Leafbirds	-0.2	-0.7	0.0	0.2
Malayan flying fox	-0.2	0.8	0.3	0.0
Porcupines	-0.4	2.1	0.0	-0.8
Bats	-0.5	1.6	1.2	0.4
Malayan Tapir	-0.5	0.5	0.2	-0.7
Wild boar	-0.5	-0.7	0.3	0.2
Parrots	-0.6	-0.8	-0.1	-0.1
Green pigeons	-0.6	-0.8	-0.1	-0.1
Bulbuls	-0.7	-0.5	-0.1	-0.2
Squirrels	-0.7	1.4	0.2	0.6
Human	-0.8	2.0	0.9	-0.4
Great Argus	-0.8	-0.3	0.1	0.2
Gaur	-1.0	-0.3	-0.6	-0.3
Ioras	-1.0	-0.6	-0.3	0.0
Mousedeers	-1.4	-0.2	0.0	0.3
Flying squirrels	-1.9	-1.0	-0.7	0.1
Colugo	-1.9	-1.1	-0.6	0.3
Doves	-1.9	0.0	-0.4	0.1
Jays	-2.0	-0.3	-0.7	-0.1
Nuthatches	-2.1	-0.3	-0.7	-0.1

Table A4.5 Overall group scores of the correlation matrix (arranged according to scores: high to low); in green (top 3), in yellow (top 10)

Animals	**PC 1**	**PC 2**	**PC 3**	**PC 4**
Gibbons	5.2	-0.8	0.9	0.1
Asian Elephant	2.9	2.0	0.9	0.0
Binturong	2.4	-1.0	-0.4	0.2
Civets	2.3	-1.3	-0.6	-0.3
Malayan sun bear	1.4	-0.1	-0.7	0.4
Macaques	1.2	-0.2	-0.3	0.5
Rats	1.2	2.7	1.1	0.4
Hornbills	0.9	0.0	0.1	-0.3
Asian fairy-bluebird	0.7	-0.8	0.0	-0.3
Barbets	0.7	-1.0	-0.1	-0.4
Langurs	0.4	-1.0	-0.1	0.1
Sambar deer	0.2	-0.9	-0.1	-0.3
Southern red muntjac	0.1	0.3	-0.7	0.2
Hill Mynah	0.0	-0.9	-0.1	-0.2
Malayan flying fox	-0.1	0.9	-0.3	0.0
Porcupines	-0.2	2.1	0.0	-0.9
Bats	-0.2	1.7	-1.2	0.4
Leafbirds	-0.2	-0.7	0.0	0.2
Malayan Tapir	-0.5	0.6	-0.2	-0.7
Squirrels	-0.5	1.5	-0.2	0.6
Human	-0.5	2.1	-0.9	-0.4
Wild boar	-0.6	-0.6	-0.3	0.2
Parrots	-0.7	-0.7	0.1	-0.1
Bulbuls	-0.7	-0.4	0.1	-0.1
Green pigeons	-0.7	-0.7	0.1	-0.1
Great Argus	-0.8	-0.2	-0.2	0.2
Gaur	-1.1	-0.2	0.5	-0.3
Ioras	-1.1	-0.5	0.3	0.1
Mousedeers	-1.4	0.0	-0.1	0.3
Doves	-1.9	0.2	0.3	0.1
Jays	-2.0	-0.1	0.6	-0.1
Flying squirrels	-2.1	-0.8	0.6	0.2
Colugo	-2.1	-0.8	0.5	0.4
Nuthatches	-2.2	-0.1	0.6	-0.1

Table A4.6 Correlations of animals considering species strength, weighted closeness, PDI and largest seed dispersed. Species strength arranged from highest to lowest: in yellow (top three) and green (above average). Correlation: in yellow (top three) and green (correlation 0.5 and above).

Animals	**Body wt. (kg)**	**Species strength**	**Gibbons**	**Elephant**	**Rats**	**Binturong**	**Macaques**	**Hornbills**
Gibbons	5.9	20.0	1.0	0.7	0.1	0.9	0.9	1.0
Asian elephant	4200	17.2	0.7	1.0	0.8	0.5	0.4	0.8
Rats	0.1	14.7	0.1	0.8	1.0	-0.2	-0.2	0.3
Binturong	21.5	8.1	0.9	0.5	-0.2	1.0	1.0	0.9
Macaques	2	6.5	0.9	0.4	-0.2	1.0	1.0	0.8
Hornbills	2.8	6.4	1.0	0.8	0.3	0.9	0.8	1.0
Civets	3.5	6.0	0.9	0.4	-0.2	1.0	1.0	0.8
Malayan sun bear	53.5	5.8	0.8	0.4	-0.2	0.9	1.0	0.8
Porcupines	8	5.4	-0.2	0.5	0.9	-0.5	-0.4	0.0
Squirrels	0.2	4.9	-0.8	-0.1	0.5	-0.8	-0.8	-0.6
Asian fairy-bluebird	0.075	4.8	0.9	0.3	-0.3	1.0	0.9	0.8
Barbets	0.041	4.2	0.8	0.2	-0.4	1.0	0.9	0.7
Langurs	7	3.8	0.6	-0.2	-0.7	0.8	0.7	0.4
Malayan flying fox	1.1	3.8	-0.4	0.2	0.6	-0.5	-0.4	-0.2
Leafbirds	0.03	3.0	-0.1	-0.8	-0.9	0.1	0.1	-0.4
Sambar deer	323	2.8	0.6	-0.1	-0.7	0.8	0.8	0.4
Muntjac	18	2.8	-0.3	-0.2	-0.2	0.0	0.1	-0.1
Hill Mynah	0.22	2.8	0.4	-0.4	-0.8	0.6	0.5	0.1
Gaur	720	2.7	-0.7	-0.6	0.0	-0.8	-0.9	-0.8
Malayan Tapir	395	2.3	-0.5	0.2	0.6	-0.6	-0.5	-0.3
Bulbuls	0.074	2.1	-0.7	-0.9	-0.5	-0.6	-0.7	-0.9
Parrots	0.18	2.0	-0.4	-0.9	-0.8	-0.3	-0.3	-0.7
Bats	0.55	1.9	-0.5	0.0	0.3	-0.5	-0.3	-0.3
Ioras	0.014	1.9	-0.7	-0.9	-0.5	-0.7	-0.7	-0.9
Human	75	1.8	-0.5	0.2	0.5	-0.5	-0.4	-0.2
Green pigeons	0.21	1.7	-0.5	-0.9	-0.7	-0.3	-0.4	-0.7
Great Argus	2	1.7	-0.9	-0.9	-0.5	-0.7	-0.7	-1.0
Wild boar	87.5	1.3	-0.5	-1.0	-0.9	-0.2	-0.2	-0.7
Jays	0.24	0.9	-0.9	-0.7	-0.1	-0.9	-0.9	-0.9
Doves	0.16	0.8	-0.9	-0.7	-0.1	-1.0	-1.0	-1.0
Mousedeers	5.3	0.7	-1.0	-0.9	-0.3	-0.9	-0.8	-1.0
Nuthatches	0.015	0.6	-0.9	-0.7	-0.1	-0.9	-0.9	-0.9
Flying squirrels	0.7	0.3	-0.8	-0.8	-0.4	-0.7	-0.8	-0.9
Colugo	1.5	0.2	-0.7	-0.9	-0.4	-0.7	-0.7	-0.9

(continued) Table A4.6 Correlations of animals considering species strength, weighted closeness, PDI and largest seed dispersed. Species strength arranged from highest to lowest: in yellow (top three) and green (above average). Correlation: in yellow (top three) and green (correlation 0.5 and above).

Animals	**Species strength**	**Civets**	**Sun bear**	**Porcupines**	**Squirrels**	**Asian fairy-bluebird**	**Barbets**
Gibbons	20.0	0.9	0.8	-0.2	-0.8	0.9	0.8
Asian Elephant	17.2	0.4	0.4	0.5	-0.1	0.3	0.2
Rats	14.7	-0.2	-0.2	0.9	0.5	-0.3	-0.4
Binturong	8.1	1.0	0.9	-0.5	-0.8	1.0	1.0
Macaques	6.5	1.0	1.0	-0.4	-0.8	0.9	0.9
Hornbills	6.4	0.8	0.8	0.0	-0.6	0.8	0.7
Civets	6.0	1.0	1.0	-0.5	-0.8	1.0	1.0
Malayan sun bear	5.8	1.0	1.0	-0.3	-0.6	0.8	0.8
Porcupines	5.4	-0.5	-0.3	1.0	0.8	-0.6	-0.7
Squirrels	4.9	-0.8	-0.6	0.8	1.0	-0.9	-1.0
Asian fairy-bluebird	4.8	1.0	0.8	-0.6	-0.9	1.0	1.0
Barbets	4.2	1.0	0.8	-0.7	-1.0	1.0	1.0
Langurs	3.8	0.8	0.6	-0.9	-1.0	0.9	0.9
Malayan flying fox	3.8	-0.5	-0.2	0.9	0.9	-0.7	-0.7
Leafbirds	3.0	0.1	0.0	-0.9	-0.6	0.3	0.4
Sambar deer	2.8	0.8	0.7	-0.9	-0.9	0.9	0.9
Muntjac	2.8	0.1	0.4	0.3	0.4	-0.2	-0.1
Hill Mynah	2.8	0.6	0.4	-1.0	-0.9	0.7	0.8
Gaur	2.7	-0.9	-1.0	0.0	0.4	-0.7	-0.7
Malayan Tapir	2.3	-0.6	-0.4	0.9	0.9	-0.8	-0.8
Bulbuls	2.1	-0.6	-0.7	-0.4	0.2	-0.5	-0.4
Parrots	2.0	-0.2	-0.4	-0.7	-0.3	-0.1	0.0
Bats	1.9	-0.4	-0.1	0.7	0.8	-0.6	-0.6
Ioras	1.9	-0.7	-0.8	-0.4	0.2	-0.5	-0.4
Human	1.8	-0.5	-0.2	0.9	0.9	-0.7	-0.7
Green pigeons	1.7	-0.3	-0.5	-0.7	-0.2	-0.2	-0.1
Great Argus	1.7	-0.7	-0.7	-0.2	0.4	-0.6	-0.6
Wild boar	1.3	-0.2	-0.2	-0.7	-0.2	-0.1	0.0
Jays	0.9	-0.9	-1.0	0.1	0.5	-0.8	-0.8
Doves	0.8	-1.0	-0.9	0.2	0.7	-0.9	-0.8
Mousedeers	0.7	-0.8	-0.8	0.0	0.5	-0.8	-0.7
Nuthatches	0.6	-0.9	-1.0	0.1	0.6	-0.8	-0.8
Flying squirrels	0.3	-0.7	-0.8	-0.3	0.2	-0.6	-0.5
Colugo	0.2	-0.7	-0.8	-0.3	0.2	-0.5	-0.5

(continues) Table A4.6 Correlations of animals considering species strength, weighted closeness, PDI and largest seed dispersed. Species strength arranged from highest to lowest: in yellow (top three) and green (above average). Correlation: in yellow (top three) and green (correlation 0.5 and above).

Animals	**Species strength**	**Langurs**	**Malayan flying fox**	**Leafbirds**	**Sambar deer**	**Muntjac**	**Hill Mynah**
Gibbons	20.0	0.6	-0.4	-0.1	0.6	-0.3	0.4
Asian Elephant	17.2	-0.2	0.2	-0.8	-0.1	-0.2	-0.4
Rats	14.7	-0.7	0.6	-0.9	-0.7	-0.2	-0.8
Binturong	8.1	0.8	-0.5	0.1	0.8	0.0	0.6
Macaques	6.5	0.7	-0.4	0.1	0.8	0.1	0.5
Hornbills	6.4	0.4	-0.2	-0.4	0.4	-0.1	0.1
Civets	6.0	0.8	-0.5	0.1	0.8	0.1	0.6
Malayan sun bear	5.8	0.6	-0.2	0.0	0.7	0.4	0.4
Porcupines	5.4	-0.9	0.9	-0.9	-0.9	0.3	-1.0
Squirrels	4.9	-1.0	0.9	-0.6	-0.9	0.4	-0.9
Asian fairy-bluebird	4.8	0.9	-0.7	0.3	0.9	-0.2	0.7
Barbets	4.2	0.9	-0.7	0.4	0.9	-0.1	0.8
Langurs	3.8	1.0	-0.8	0.7	1.0	-0.1	1.0
Malayan flying fox	3.8	-0.8	1.0	-0.8	-0.8	0.6	-0.9
Leafbirds	3.0	0.7	-0.8	1.0	0.7	-0.2	0.9
Sambar deer	2.8	1.0	-0.8	0.7	1.0	-0.1	0.9
Muntjac	2.8	-0.1	0.6	-0.2	-0.1	1.0	-0.2
Hill Mynah	2.8	1.0	-0.9	0.9	0.9	-0.2	1.0
Gaur	2.7	-0.4	0.0	0.3	-0.4	-0.4	-0.1
Malayan Tapir	2.3	-0.9	1.0	-0.8	-0.9	0.5	-0.9
Bulbuls	2.1	0.0	-0.3	0.7	-0.1	-0.2	0.3
Parrots	2.0	0.4	-0.6	0.9	0.4	-0.3	0.6
Bats	1.9	-0.7	0.9	-0.6	-0.7	0.8	-0.7
Ioras	1.9	-0.1	-0.3	0.6	-0.1	-0.3	0.2
Human	1.8	-0.9	1.0	-0.8	-0.8	0.6	-0.9
Green pigeons	1.7	0.3	-0.5	0.9	0.3	-0.2	0.6
Great Argus	1.7	-0.2	0.1	0.5	-0.2	0.2	0.1
Wild boar	1.3	0.4	-0.4	0.9	0.4	0.2	0.6
Jays	0.9	-0.5	0.1	0.2	-0.5	-0.2	-0.2
Doves	0.8	-0.6	0.3	0.2	-0.6	-0.1	-0.3
Mousedeers	0.7	-0.4	0.2	0.4	-0.4	0.1	-0.1
Nuthatches	0.6	-0.5	0.1	0.2	-0.5	-0.2	-0.2
Flying squirrels	0.3	-0.1	-0.2	0.6	-0.2	-0.3	0.1
Colugo	0.2	-0.1	-0.2	0.6	-0.1	-0.3	0.2

(continued) Table A4.6 Correlations of animals considering species strength, weighted closeness, PDI and largest seed dispersed. Species strength arranged from highest to lowest: in yellow (top three) and green (above average). Correlation: in yellow (top three) and green (correlation 0.5 and above).

Animals	**Species strength**	**Gaur**	Malayan Tapir	**Bulbuls**	**Parrots**	**Bats**	**Ioras**
Gibbons	20.0	-0.7	-0.5	-0.7	-0.4	-0.5	-0.7
Asian Elephant	17.2	-0.6	0.2	-0.9	-0.9	0.0	-0.9
Rats	14.7	0.0	0.6	-0.5	-0.8	0.3	-0.5
Binturong	8.1	-0.8	-0.6	-0.6	-0.3	-0.5	-0.7
Macaques	6.5	-0.9	-0.5	-0.7	-0.3	-0.3	-0.7
Hornbills	6.4	-0.8	-0.3	-0.9	-0.7	-0.3	-0.9
Civets	6.0	-0.9	-0.6	-0.6	-0.2	-0.4	-0.7
Malayan sun bear	5.8	-1.0	-0.4	-0.7	-0.4	-0.1	-0.8
Porcupines	5.4	0.0	0.9	-0.4	-0.7	0.7	-0.4
Squirrels	4.9	0.4	0.9	0.2	-0.3	0.8	0.2
Asian fairy-bluebird	4.8	-0.7	-0.8	-0.5	-0.1	-0.6	-0.5
Barbets	4.2	-0.7	-0.8	-0.4	0.0	-0.6	-0.4
Langurs	3.8	-0.4	-0.9	0.0	0.4	-0.7	-0.1
Malayan flying fox	3.8	0.0	1.0	-0.3	-0.6	0.9	-0.3
Leafbirds	3.0	0.3	-0.8	0.7	0.9	-0.6	0.6
Sambar deer	2.8	-0.4	-0.9	-0.1	0.4	-0.7	-0.1
Southern red muntjac	2.8	-0.4	0.5	-0.2	-0.3	0.8	-0.3
Hill Mynah	2.8	-0.1	-0.9	0.3	0.6	-0.7	0.2
Gaur	2.7	1.0	0.1	0.9	0.6	-0.1	0.9
Malayan Tapir	2.3	0.1	1.0	-0.2	-0.6	0.9	-0.2
Bulbuls	2.1	0.9	-0.2	1.0	0.9	-0.1	1.0
Parrots	2.0	0.6	-0.6	0.9	1.0	-0.4	0.9
Bats	1.9	-0.1	0.9	-0.1	-0.4	1.0	-0.2
Ioras	1.9	0.9	-0.2	1.0	0.9	-0.2	1.0
Human	1.8	0.0	1.0	-0.2	-0.6	1.0	-0.2
Green pigeons	1.7	0.7	-0.5	0.9	1.0	-0.4	0.9
Great Argus	1.7	0.8	0.1	0.9	0.8	0.2	0.9
Wild boar	1.3	0.4	-0.4	0.8	0.9	-0.1	0.8
Jays	0.9	1.0	0.2	0.9	0.6	0.1	0.9
Doves	0.8	0.9	0.4	0.8	0.5	0.3	0.8
Mousedeers	0.7	0.8	0.3	0.9	0.7	0.3	0.9
Nuthatches	0.6	1.0	0.3	0.9	0.6	0.1	0.9
Flying squirrels	0.3	0.9	-0.1	1.0	0.8	-0.1	1.0
Colugo	0.2	0.9	-0.1	1.0	0.9	-0.1	1.0

(continued) Table A4.6 Correlations of animals considering species strength, weighted closeness, PDI and largest seed dispersed. Species strength arranged from highest to lowest: in yellow (top three) and green (above average). Correlation: in yellow (top three) and green (correlation 0.5 and above).

Animals	**Species strength**	**Human**	**Green pigeons**	**Great Argus**	**Wild boar**	**Jays**	**Doves**
Gibbons	20.0	-0.5	-0.5	-0.9	-0.5	-0.9	-0.9
Asian Elephant	17.2	0.2	-0.9	-0.9	-1.0	-0.7	-0.7
Rats	14.7	0.5	-0.7	-0.5	-0.9	-0.1	-0.1
Binturong	8.1	-0.5	-0.3	-0.7	-0.2	-0.9	-1.0
Macaques	6.5	-0.4	-0.4	-0.7	-0.2	-0.9	-1.0
Hornbills	6.4	-0.2	-0.7	-1.0	-0.7	-0.9	-1.0
Civets	6.0	-0.5	-0.3	-0.7	-0.2	-0.9	-1.0
Malayan sun bear	5.8	-0.2	-0.5	-0.7	-0.2	-1.0	-0.9
Porcupines	5.4	0.9	-0.7	-0.2	-0.7	0.1	0.2
Squirrels	4.9	0.9	-0.2	0.4	-0.2	0.5	0.7
Asian fairy-bluebird	4.8	-0.7	-0.2	-0.6	-0.1	-0.8	-0.9
Barbets	4.2	-0.7	-0.1	-0.6	0.0	-0.8	-0.8
Langurs	3.8	-0.9	0.3	-0.2	0.4	-0.5	-0.6
Malayan flying fox	3.8	1.0	-0.5	0.1	-0.4	0.1	0.3
Leafbirds	3.0	-0.8	0.9	0.5	0.9	0.2	0.2
Sambar deer	2.8	-0.8	0.3	-0.2	0.4	-0.5	-0.6
Southern red muntjac	2.8	0.6	-0.2	0.2	0.2	-0.2	-0.1
Hill Mynah	2.8	-0.9	0.6	0.1	0.6	-0.2	-0.3
Gaur	2.7	0.0	0.7	0.8	0.4	1.0	0.9
Malayan Tapir	2.3	1.0	-0.5	0.1	-0.4	0.2	0.4
Bulbuls	2.1	-0.2	0.9	0.9	0.8	0.9	0.8
Parrots	2.0	-0.6	1.0	0.8	0.9	0.6	0.5
Bats	1.9	1.0	-0.4	0.2	-0.1	0.1	0.3
Ioras	1.9	-0.2	0.9	0.9	0.8	0.9	0.8
Human	1.8	1.0	-0.5	0.1	-0.3	0.1	0.3
Green pigeons	1.7	-0.5	1.0	0.8	0.9	0.7	0.6
Great Argus	1.7	0.1	0.8	1.0	0.8	0.8	0.9
Wild boar	1.3	-0.3	0.9	0.8	1.0	0.5	0.5
Jays	0.9	0.1	0.7	0.8	0.5	1.0	1.0
Doves	0.8	0.3	0.6	0.9	0.5	1.0	1.0
Mousedeers	0.7	0.2	0.7	1.0	0.7	0.9	0.9
Nuthatches	0.6	0.2	0.7	0.9	0.5	1.0	1.0
Flying squirrels	0.3	-0.2	0.9	0.9	0.7	0.9	0.9
Colugo	0.2	-0.2	0.9	0.9	0.7	0.9	0.9

(continued) Table A4.6 Correlations of animals considering species strength, weighted closeness, PDI and largest seed dispersed. Species strength arranged from highest to lowest: in yellow (top three) and green (above average). Correlation: in yellow (top three) and green (correlation 0.5 and above).

Animals	**Species strength**	**Mousedeers**	**Nuthatches**	**Flying squirrels**	**Colugo**
Gibbons	20.0	-1.0	-0.9	-0.8	-0.7
Asian Elephant	17.2	-0.9	-0.7	-0.8	-0.9
Rats	14.7	-0.3	-0.1	-0.4	-0.4
Binturong	8.1	-0.9	-0.9	-0.7	-0.7
Macaques	6.5	-0.8	-0.9	-0.8	-0.7
Hornbills	6.4	-1.0	-0.9	-0.9	-0.9
Civets	6.0	-0.8	-0.9	-0.7	-0.7
Malayan sun bear	5.8	-0.8	-1.0	-0.8	-0.8
Porcupines	5.4	0.0	0.1	-0.3	-0.3
Squirrels	4.9	0.5	0.6	0.2	0.2
Asian fairy-bluebird	4.8	-0.8	-0.8	-0.6	-0.5
Barbets	4.2	-0.7	-0.8	-0.5	-0.5
Langurs	3.8	-0.4	-0.5	-0.1	-0.1
Malayan flying fox	3.8	0.2	0.1	-0.2	-0.2
Leafbirds	3.0	0.4	0.2	0.6	0.6
Sambar deer	2.8	-0.4	-0.5	-0.2	-0.1
Southern red muntjac	2.8	0.1	-0.2	-0.3	-0.3
Hill Mynah	2.8	-0.1	-0.2	0.1	0.2
Gaur	2.7	0.8	1.0	0.9	0.9
Malayan Tapir	2.3	0.3	0.3	-0.1	-0.1
Bulbuls	2.1	0.9	0.9	1.0	1.0
Parrots	2.0	0.7	0.6	0.8	0.9
Bats	1.9	0.3	0.1	-0.1	-0.1
Ioras	1.9	0.9	0.9	1.0	1.0
Human	1.8	0.2	0.2	-0.2	-0.2
Green pigeons	1.7	0.7	0.7	0.9	0.9
Great Argus	1.7	1.0	0.9	0.9	0.9
Wild boar	1.3	0.7	0.5	0.7	0.7
Jays	0.9	0.9	1.0	0.9	0.9
Doves	0.8	0.9	1.0	0.9	0.9
Mousedeers	0.7	1.0	0.9	0.9	0.9
Nuthatches	0.6	0.9	1.0	0.9	0.9
Flying squirrels	0.3	0.9	0.9	1.0	1.0
Colugo	0.2	0.9	0.9	1.0	1.0

Figure A4.01 The Royal Belum State Park landscape, and the Belum-Temengor lake.

Figure A4.02 Woody debris in the Belum-Temengor lake proposed to have compensated for lost nutrients and minimized the functional impacts of the dam (Hashim, 2013).

Figure A4.03 Elephant utilizing the Belum-Temengor lake along the forest edge.

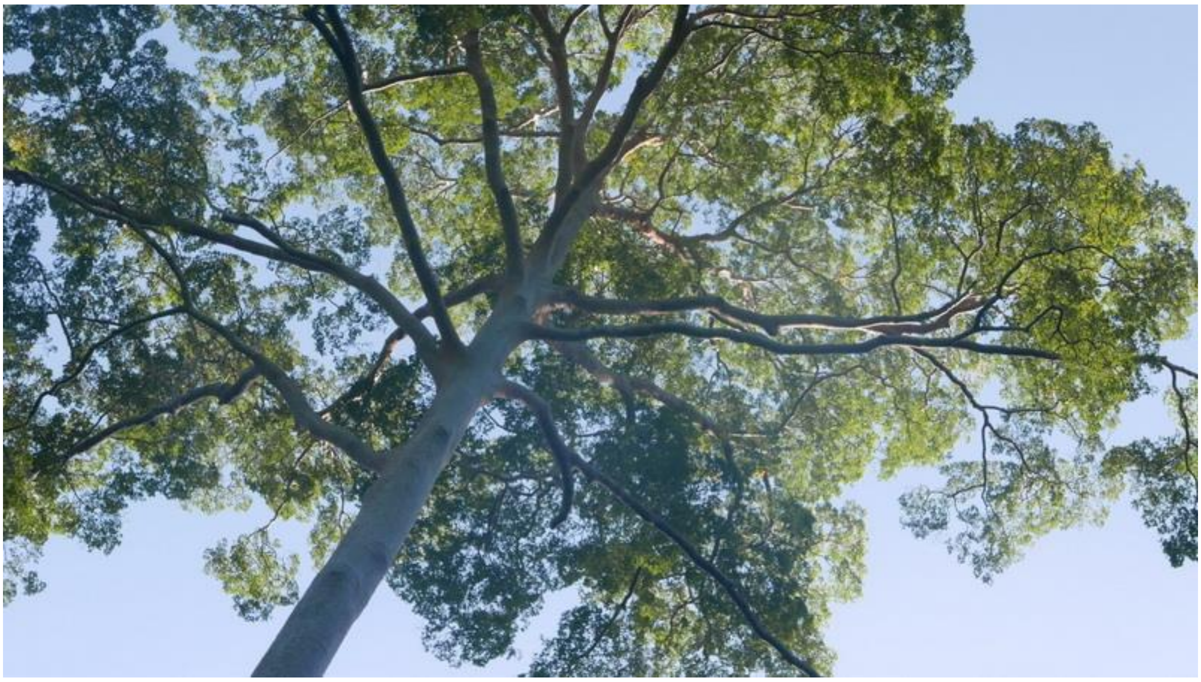


Figure A4.04 Large emergent tree in the forest.

Figure A4.05 Elephant footprints along the successional zone.

Figure A4.06 Tiger footprint along the river.

Figure A4.07 Field assistant Cherang (left) and I searching for fruits in an interaction quadrat.

Figure A4.08 Seed predation of the *Shorea sp.* (Dipterocarpaceae) seeds.

Figure A4.09 Signs of megafaunal syndrome fruit*, Calophyllum macrocarpum* (Calophyllaceae) lacking seed dispersers.

Figure A4.10 Teeth mark of the flying fox (left) on *Calophyllum macrocarpum* and nuts of *Lithocarpus sp.* (Fagaceae) eaten by squirrels (right).

Figure A4.11 Bertam, *Eugeissona sp.* (Arecaceae) infructescene broken by elephants.

Figure A4.12 Field assistant Ridzuan setting up a camera trap.

Figure A4.13 Research assistant Vivienne setting up camera trap fruit baits of *Citrus halimii* (Rutaceae).

Figure A4.14 Fruits of different sizes collected from transects.

Figure A4.15 Bear defecation

Figure A4.16 Elephant dung

Figure A4.17 LEK Interviews of seed dispersal interactions with Orang Asli participants. Beracut Bin Lebak (left) and Arrifyn Bin Dris (right) from Kampung Darmai.

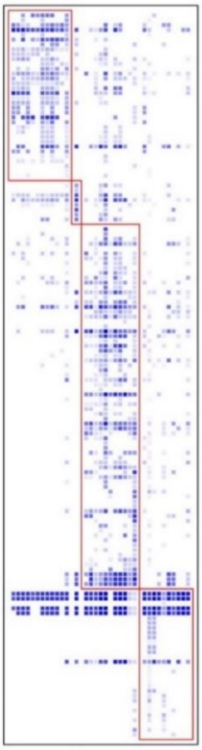


Figure A4.18 Network with a nested structure. Matrix was distinguished as four modules. Each square represents a pairwise interaction between a plant (row) and an animal (column). The intensity of blue represents interaction weightage of how frequently local indigenous people observed the interactions.

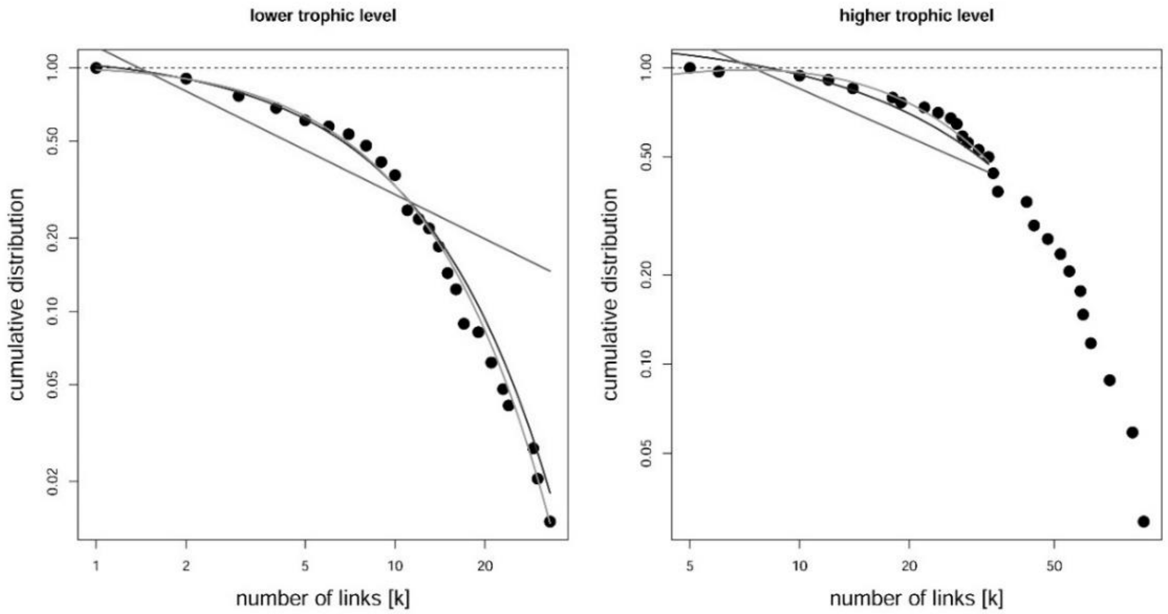


Figure A4.19 Cumulative distributions of (left) lower trophic plants and (right) higher trophic animals' network. Black line represents exponential, dark grey represents power law and light grey represents truncated power-law fits.

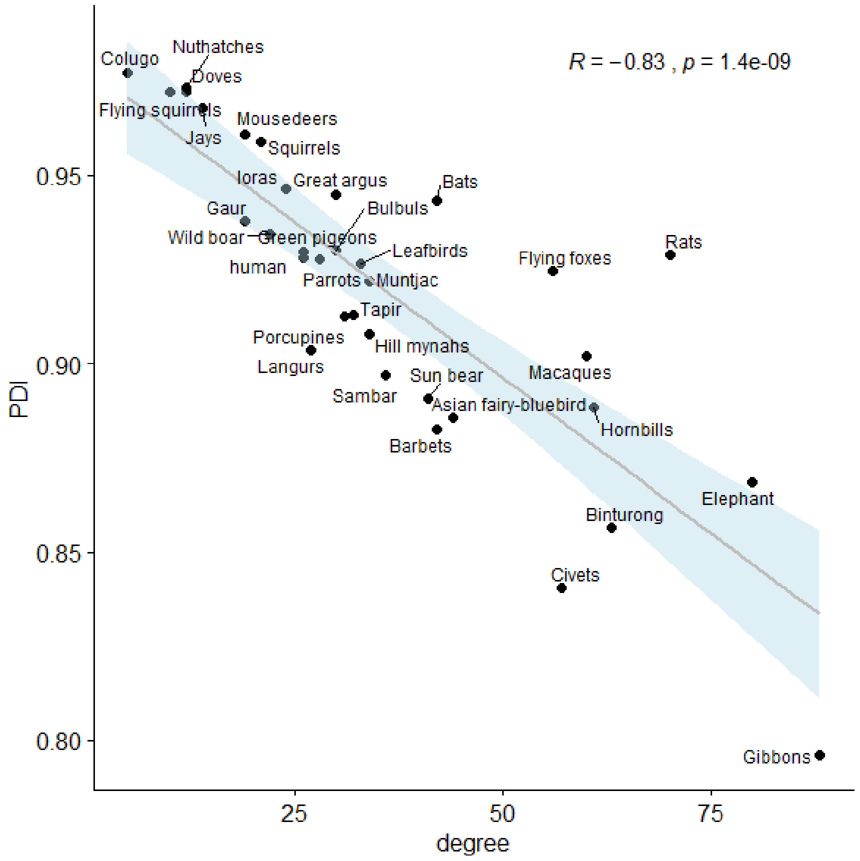


Figure A4.20 Correlations of nestedness (left) and species strength (right) to degree

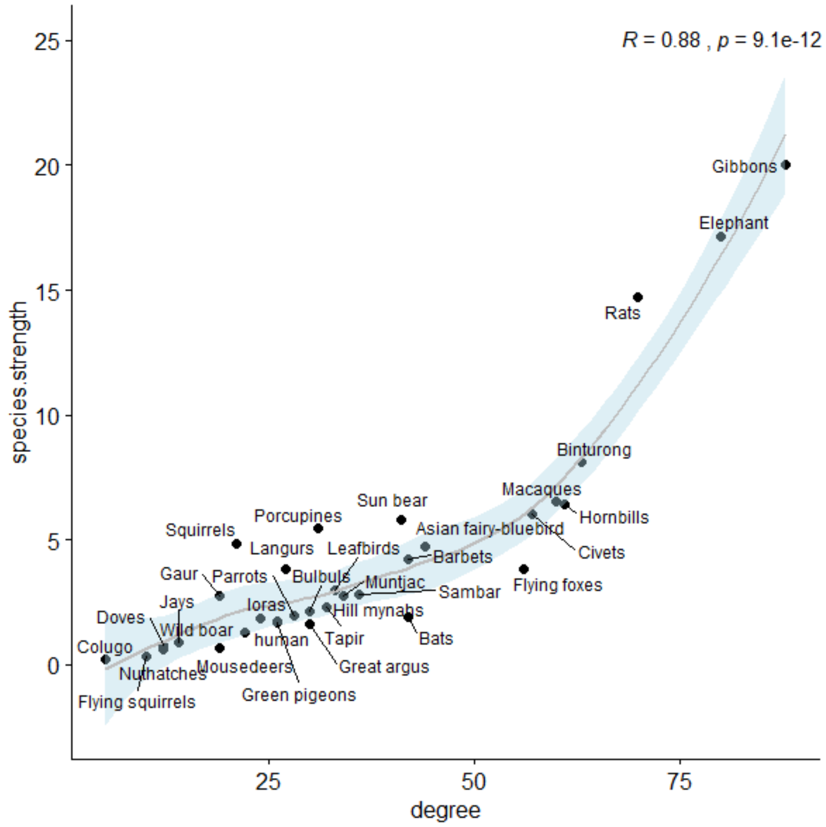


Figure A4.21 Correlations of species strength to degree

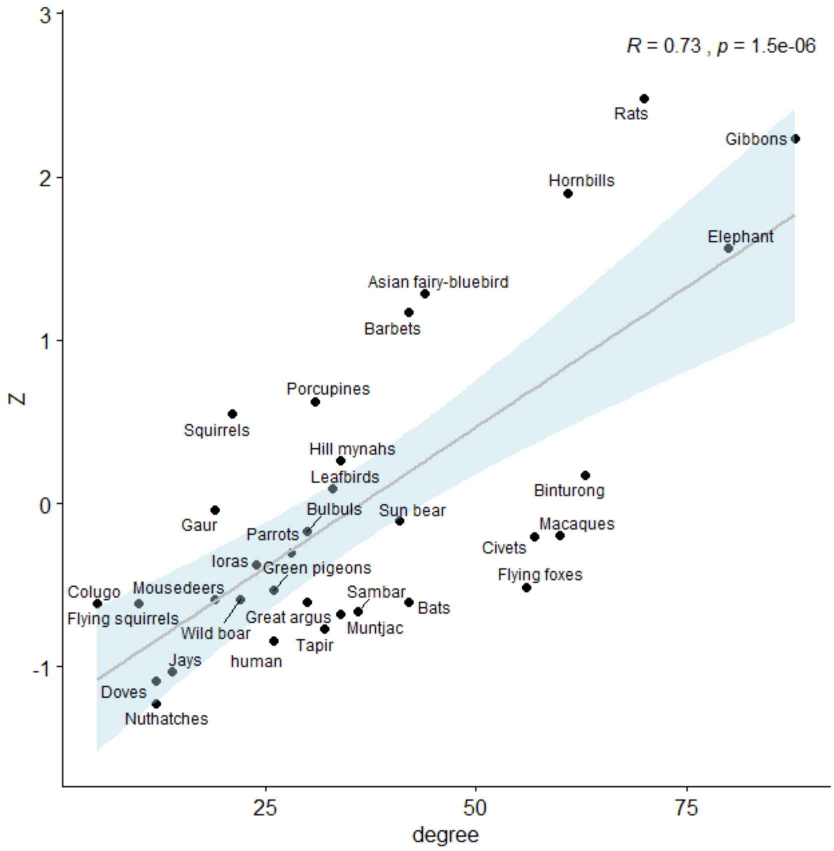


Figure A4.22 Correlations of *z* values to degree

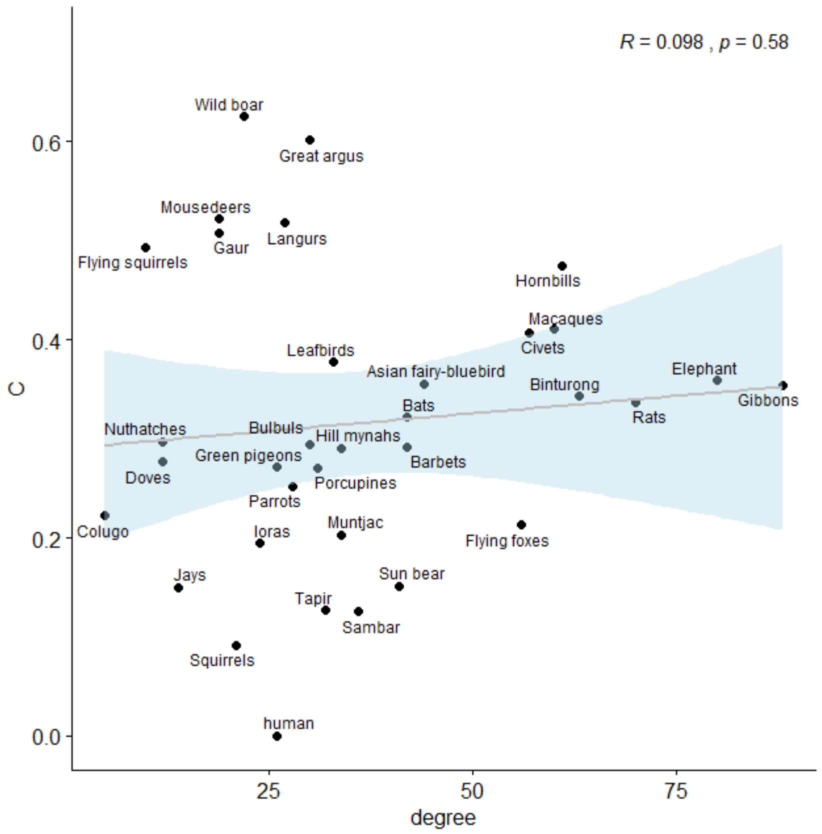


Figure A4.23 Correlations of *c* values to degree

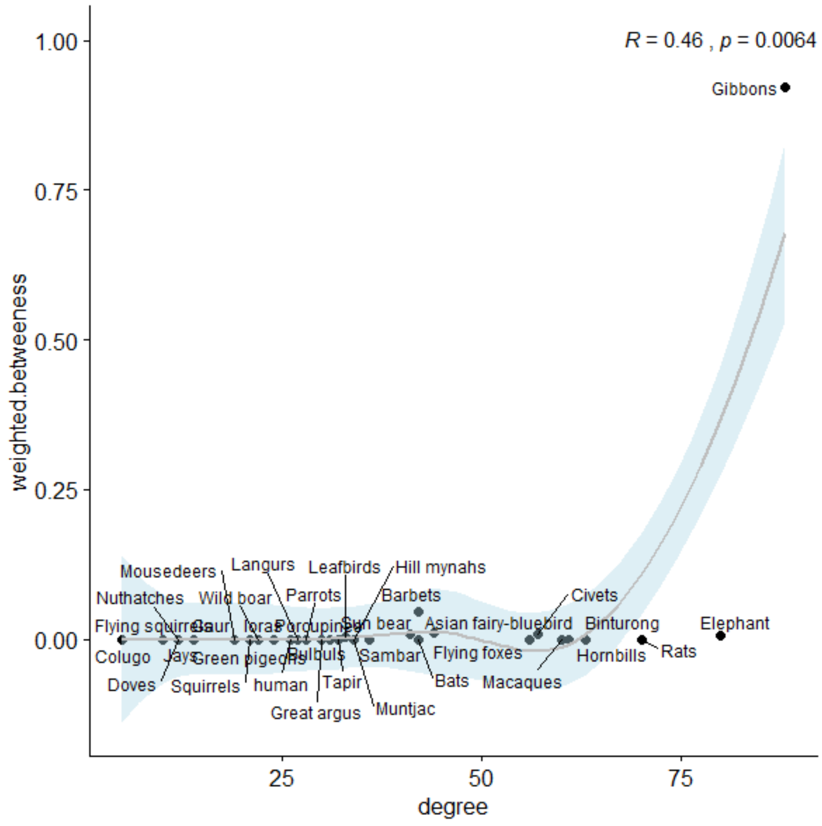


Figure A4.24 Correlations of weighted betweenness to degree

CHAPTER FIVE

GENERAL DISCUSSION

Key Findings and Future Studies

The ecology, biology, and cultural importance of Asian elephants have been well-synthesized by Sukumar (2003) in his book "The Living Elephants". In the dipterocarp rainforests of Sundaland, we are missing information on how elephants are affecting ecosystem processes and the services they provide through their interactions with their environment. While important studies have been made concerning the Asian elephants in Malaysia (e.g. Olivier, 1978; Estes et al., 2012; English et al., 2014a, 2014b; Yamamoto-Ebina et al., 2016; Hii, 2017; Tan, 2017; Wong, 2017; Wadey et al., 2019; de la Torre et al., 2019) and the services they provide (Kromann-Clausen, 2015; Tan et al., unpubl.), my review in chapter one showed the role of Asian elephants as ecosystem engineers or keystone species is not well-supported in comparison to the African elephants. This leaves much space for improvement in the research direction of the effects of elephants on its environment. In addition to Asian elephants, many other species have not received sufficient research attention to support their protection. This includes basic data on frugivory and seed dispersal which is necessary to identify the important services different animals provide. Some species can be more important and vulnerable than others due to anthropogenic factors such as poaching and hunting (Corlett, 2007; Dirzo et al., 2014; Bovendorp et al., 2018).

This thesis has four main themes concerning Asian elephants — including diet selection (chapter two), herbivory impacts (chapter two), frugivory (chapter three), and the seed dispersal role of the Asian elephant in the community (chapter four). While I investigated the ecological function of Asian elephants, I also provided a bigger picture showing how other fruit-eating animals are interacting in the dipterocarp rainforest community. A community-oriented study is crucial as we are facing fast-paced defaunation and biodiversity loss(Dirzo et al., 2014). The ecological niches of living organisms and the interconnections that connect them are difficult to discern unless we can view them from an ecosystem perspective.

As part of our collaborations (refer to Terborgh et al., 2018) to investigate the influence of elephant herbivory on the structure of closed-canopy forests, in chapter two of my thesis, I investigated the diet and food preference of the Asian elephant and their herbivory impact on different plant stems. Asian elephants highly preferred monocots particularly palms (preference ratio, PR=4.6) that are not abundant in the forest. Hindgut fermentation allowed the monogastric elephant to consume palms (39%) and dicots (20% lianas, 30% trees) as their principal diet. Where monocots can be found, most sustained high damages (above 40% of measured stems in foraged patches). Their feeding behaviour was associated with a reduced palm density in the Royal Belum rainforest where elephants roam, as compared to Krau, a forest which has been without elephants since 1993. Large tree saplings (27%, n=11 patches) of around 2 ±1 cm were vulnerable to elephant damage. For elephants to contribute to the physiognomy of the rainforest, a large proportion of stems broken by them need to die off. Simulating elephant breaks by manually cutting saplings, Terborgh et al. (unpubl.) found around 90% of the cut stems resprouted after 13.5 months. These high recovery rates indicated the possibility of low impacts by elephants on forest structure. Ickes et al. (2003) found a similar recovery in stems damaged by wild boars after 6 months. However, this survivorship eventually decreased to 65% after 36 months, suggesting the need to observe the survivorship of elephant stem breaks over a longer period. Common tree species were linked to higher resprouting ability as compared to rare species in some forests (Matelson et al., 1995; Guariguata, 1998). Further studies of resprouting ability between species would enable us to detect possible elephant-initiated shifts of forest composition. From direct observations of captive wild elephants, around 0–30% of tree seedlings or saplings could be uprooted during feeding. The consequences of this high variability in the frequency of uprooting stems can be explored further as both stem-breaking and uprooting could lead to long-term differences in the growth rates of plants (Berzaghi et al., 2019). Since wild boars have a huge impact on stems (Ickes et al., 2003), the effects of elephant herbivory are unlikely to be the sole contributor to reduced sapling density in the Sundaic dipterocarp rainforests. To determine Asian elephants' impact on the forest dynamics, the effects of pigs (Ickes et al., 2003), and the resprouting ability of different plant species need to be included in the picture and investigated over longer terms.

My work in chapter two contributed partly to our overall understanding of the elephant's role in the rainforest structure, but there remains much that needs to be explored. The implications of the elephant's food preferences to human-elephant conflict (HEC) is discussed under the 'Implications and Recommendations to Explore' section of this chapter.

Available seed dispersal studies showed the importance of Asian elephants in dispersing seeds (Campos-Arceiz et al., 2008a; Campos-Arceiz & Blake, 2011; Sekar et al., 2016). Fewer studies have recorded interactions between Asian elephants and other seed dispersers with wild fruiting species (Sekar et al., 2016; McConkey et al., 2018). Chapter three of my thesis provided a fundamental understanding of Asian elephants in the frugivory and seed dispersal of a mast-fruiting tree, the *Irvingia malayana.* Rare interactions of a large-fruit fleshy plant species with the animal community were observed. Albeit the removal rate of fruits by elephants was low, results suggested elephants as the most important terrestrial seed disperser for *Irvingia malayana.* Seed dispersal by elephants allowed the *Irvingia malayana* to escape from effective seed predation by the wild boars. Germination experiments indicated the high viability of elephant dispersed seeds. As observed in highly utilised salt licks, seeds swallowed by elephants were efficiently dispersed (personal observations). Without the Asian elephants, such large-fruited species could be less efficiently dispersed in the forest, with compromised dispersal fitness. Future studies can target a higher number of fruiting trees, conduct tree watches or canopy camera trapping, carry out more regular camera checks, and clearly evaluate the seed dispersal effectiveness (quantity and quality) of large-fruited plant species such as the *Irvingia malayana.*

As highly interactive generalists, megafauna require a community or ecosystem approach to understand their functions (Dudley,1993). The key finding of this thesis (Chapter four) was the identification of a novel role of elephants at a community level in a Sundaic dipterocarp rainforest. Globally, the lack of network studies is particularly acute in tropical ecosystems involving large vertebrates (Vidal et al., 2013). Using an inter-disciplinary approach, I built a seed dispersal network through the combination of ecological knowledge (LEK), feeding signs and camera trapping, and published records. Apart from distinguishing the various modules of the seed dispersal network, the key feature to the seed dispersal community was network nestedness, an interaction pattern at the community level that promoted the persistence of less-connected species. As a result, I identified key seed dispersers as gibbons, Asian elephant, binturong, civets (as a large taxonomic group), and sun bear.

The identification of important species in the ecosystem is a persisting challenge to conservationists and network ecologists (Bond, 1994; Mello et al., 2015; Escribano-Avila et al., 2018). Results from chapter 4 provide a crucial reference for identifying key terrestrial mammals that require protection if a resilient seed dispersal network is to be maintained. In the community, gibbons were the most efficient seed dispersers for plant species central to the network. Multiple network indices indicated their importance both to the maintenance of the network structure and the plants they interact with. Despite their important role as seed dispersers, gibbons are endangered (IUCN, 2008) and are still being illegally hunted in Malaysia. Gibbons require high attention and protection in Peninsular Malaysia. Asian elephants stood out as dominant functional generalists, dispersing fruits both central to the network and the less commonly dispersed large-seeded species. They complement gibbons in seed dispersal, and introduced dispersal variability and diversity to the network together with rats (as a large taxonomic group) that disperse seeds through their hoarding ability. Asian elephants are also endangered (IUCN, 2008) and one of the last remaining megaherbivores, other than gaur, of Peninsular Malaysia. Both gibbons and elephants promoted functional redundancy of the seed dispersal network but their roles are not replaceable by a single less efficient or functionally specialised species. To determine if gibbons or elephants are keystone species in this ecosystem, changes in seed dispersal dynamics can be assessed following the simulation of their extinction (Power et al., 1996; Khanina, 1998; Sinclair & Byrom, 2006). This can be further explored in future studies.

The effects of defaunation are of the highest concern for biodiversity conservation (Dirzo et al., 2014; Bovendorp et al., 2018; Chanthorn et al., 2019). In chapter four, I presented the first scenario of the functional coextinction of a highly diverse system in a Sundaic dipterocarp rainforest. The loss of vulnerable but highly connected species saw rapid co-extinction of their plant partners. The results reflected the vulnerability of the seed dispersal function and the urgent need to protect vulnerable (IUCN) but highly functional animal species. It highlighted the importance of consistent recording and preserving plant-animal interactions apart from species-focussed studies. If we neglect this, we will lose information that is critical to habitat or seed dispersal service maintenance, and even fundamental information (e.g. target foodplants) required to conserve a species. I only provided snapshots of the defaunation consequences. Cryptic ecological functions are often degraded prior to the threats of species' existence (Dirzo et al., 2014; McConkey & O’Farrill, 2016). Urgent efforts are required to investigate how vulnerable the Belum network is, rather than inferring robustness from the current network. I hope to be able to carry out a comprehensive investigation of the status of the actual network to determine the effects of defaunation in future studies.

Challenges of Using New Methods

Applying an interdisciplinary method to obtain a representative network was highly challenging. I explained the problems I encountered under “Methods: assignment of seed dispersal interactions”. The process involved multiple trial-and-error attempts before deriving the final methods described. I made decisions to balance between a well-represented network matrix (having most plants with at least 1 interaction) and accuracy (to be fair with the representation, see methods). Apart from bias representation due to unequal sets of LEK information obtained, it was necessary to experiment with both weighted and non-weighted networks and to select out useful network indices to describe the system.

During the early developmental stage of the networks, I tried to be conservative, sticking to non-weighted networks. As part of the objective of the network was to include different forms of seed dispersal such as seed hoarding in which dispersal distance is short and germination success is low, a non-weighted network would have resulted in some species being over-represented in their seed dispersal capabilities. Hence, I created multiple non-weighted networks to describe the system. I experimented with several methods of assigning interactions using different combinations of LEK and published information. One of them was assigning interactions sequentially according to seed treatment by animals (e.g. hoarding was only assigned an interaction when no other forms of dispersal mode were available). Another way was to assign interactions using combinations that could represent chances of dispersal — counting the number of LEK information, how often the interaction was indicated as common, the seed dispersal modes, etc. I created different networks that described different dispersal scenarios such as frugivory, seed swallowing, and a network that represented dispersal chances. While the networks were presentable, both the methods and results were difficult to interpret. In the final network, while the methods described in the formation of this final matrix were lengthy and subjective, it is a matrix that balanced between easy interpretation and reliability.

With direct observations of interactions, the trial and error process of network matrix combination, including an extensive check of published records, is not necessary. A large amount of my time in the Ph.D. was spent to achieve this. Despite the effort needed for this method, it would have taken a much longer period, resource, and manpower to build such a diverse network using direct observations. To have a more complete understanding of the effects of species extinction, I also experimented with different ways of simulating defaunation — checking for changes in network indices following the removal of individual species, the most important species, and the sequential removal of vulnerable species. To better understand the network indices, I observed how different network indices changed following the removal of each species. For example, whether they would increase or decrease in more simplified systems. Amongst the array of network indices available, I selected useful indices that would help explain the patterns of the networks. I compared the differences and trends between the frugivory and seed dispersal networks. Due to the complexity of the system, my supervisors and I decided that more work is needed to better represent the current defaunation scenario and I was unable to dedicate a chapter to the consequences of defaunation. Nonetheless, I presented coextinction results with algorithms used by other authors (Dunne et al., 2002; Memmott et al., 2004; Dormann et al., 2016).

Unpublished as a chapter in this thesis., my field-team and I monitored the fruiting phenology of the Royal Belum State Park for sixteen months. To accomplish the network study, it is possible to collect fruit samples and interaction data, ignoring the systematic recording of phenology and the use of interaction quadrats. Although not the backbone of this thesis, I persisted in the efforts of putting phenology into records to provide a basic reference for the conservation of a broad community — both plants and animals. Phenology data adds value to a better understanding of plant-animal interactions, food availability for animals and may allow us to advance the network studies into temporal series to address dynamics (Bascompte & Jordano, 2014). I identified trends in 164 plant species belonging to 42 fruiting plant families (Figure 5.1 and 5.2), as well as food availability for different animal taxa described in the networks (Figure 5.3 and 5.4), that included a La Niña year in 2016. Plants that fruited abundantly with La Niña included the Dipterocarpaceae, Fabaceae, Combretaceae, Ebenaceae, and Moraceae families, of which Ebenaceae and Moraceae are fleshy fruits, and Fabaceae were highly consumed by primates, rodents, and wild boars. Results from chapter four showed plants from the Moraceae family included the most important species — *Ficus* and *Artocarpus*. Fluctuations in fruiting could lead to large impacts on the animal community, such that animals may face lower food availability in between masting periods that coincides with climatic events such as the La Niña or El Niño. Severe food scarcity has had negative effects on large animals such as sun bears and bearded pigs (Wright et al., 1999; Curran & Leighton, 2000; Wong et al., 2005; Fredriksson et al., 2006). Over the sampling period, July was the fruiting peak in terms of species diversity and the number of individuals of fruiting trees, while December was the lean period when fruit availability was at its lowest for all animals. Some families such as Annonaceae, and several large-fruited species such as Apocynaceae and Calophyllaceae appeared to be unaffected by the effects of La Niña, and some fruited out of the annual fruiting peak. During the lean period, some animals might be facing stress from food scarcity. Mitigation methods can be further explored for the conservation of species vulnerable to food scarcity by introducing habitat changes that could facilitate productivity for these animals. The phenology data needs to be analysed in detail, and according to the food available for different animal groups to derive more useful interpretations.

It was a pity to discontinue the fruiting phenology study due to budget constraints. Phenology requires long-term monitoring to observe a more explicit and larger picture (more than 5–10 years) of the system. I propose the establishment of permanent plots or transects in BTFC that include the collection of plant-animal interactions in the studies. In general, it is important to monitor phenology while carrying out animal-related studies and vice versa.

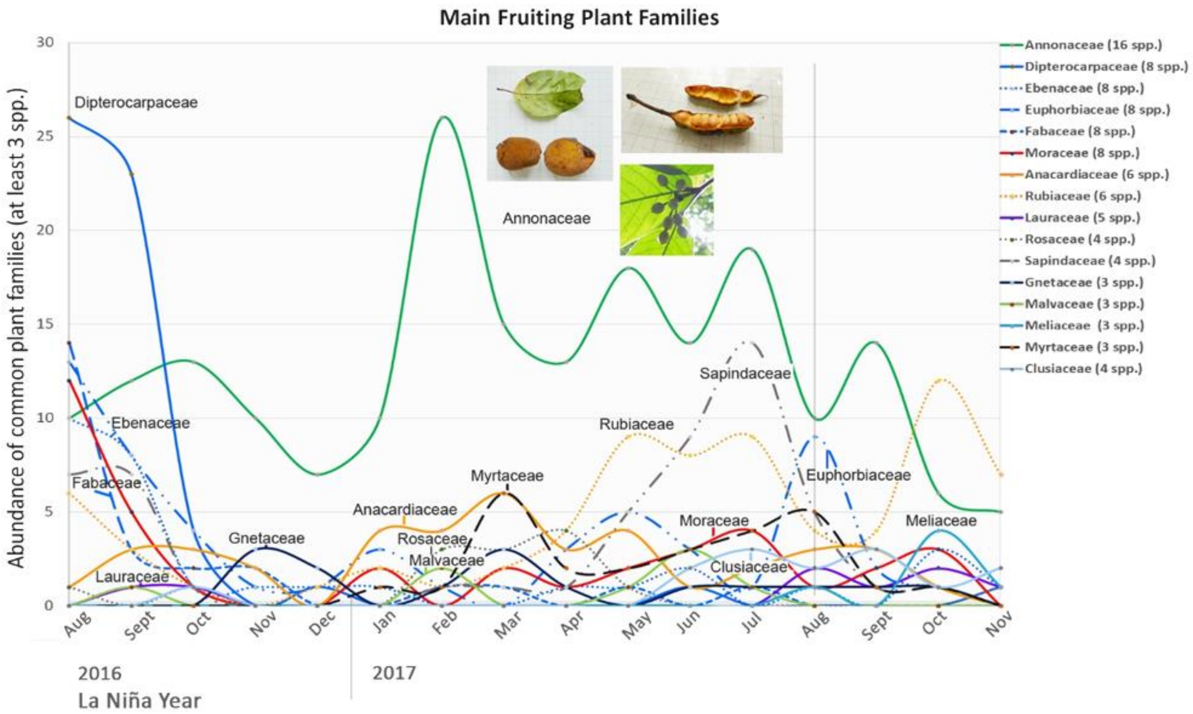


Figure 5.1 Abundance of families of plants with at least three species that fruited over 16 months.

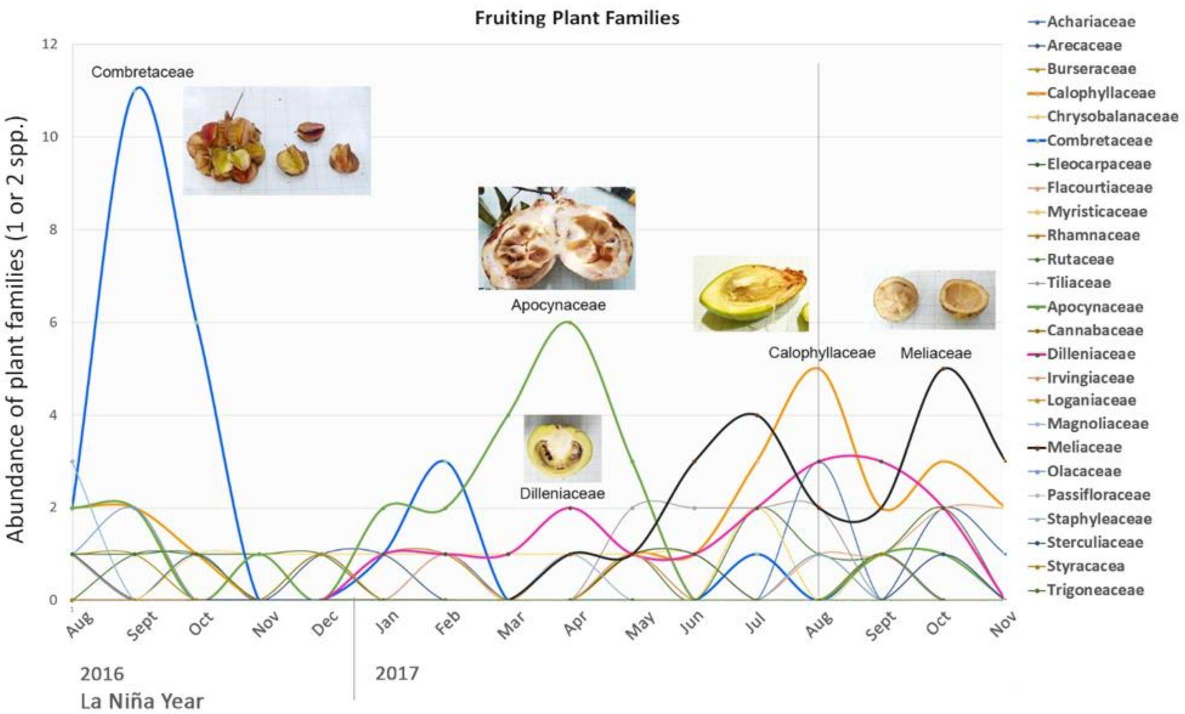


Figure 5.2 Abundance of families of plants with at least one or two species that fruited over 16 months.

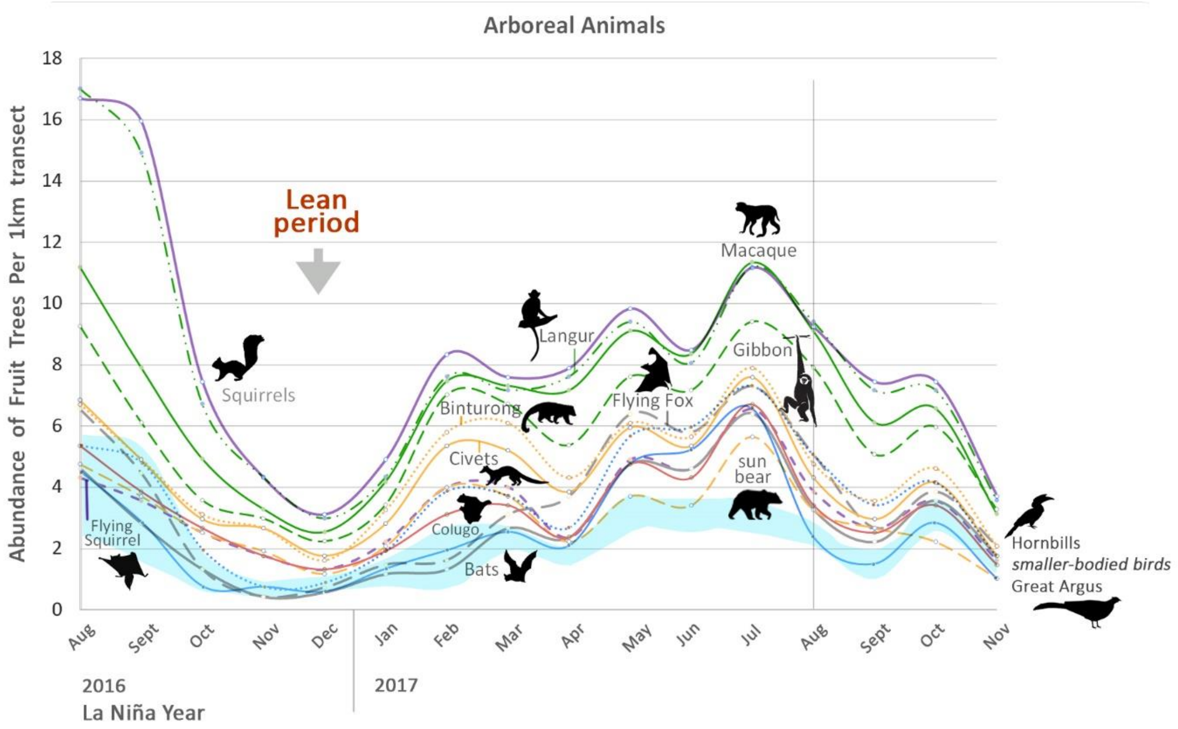


Figure 5.3 Abundance of fruit trees available for birds and arboreal mammals over 16 months

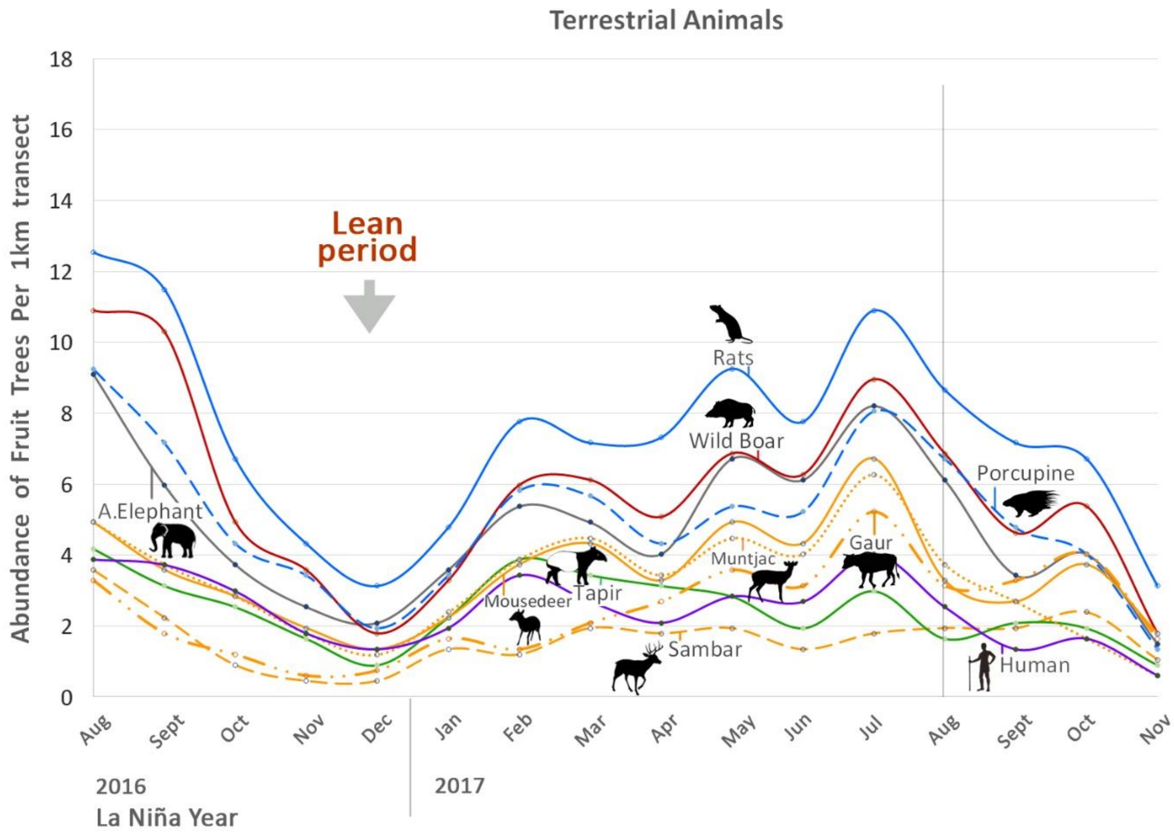


Figure 5.4 Abundance of fruit trees available for terrestrial mammals over 16 months

Implications and Recommendations to Explore

In this study, Asian elephants strongly preferred monocots, particularly palms. They damaged tree saplings at an average diameter of 1.7±1.1 cm (range 0.2—7.1cm), broken at an average height of 1.1 ± 0.5 m (range = 0.1–2.8 m). This would inevitably lead to frequent conflicts with humans in plantations. The current method employed to deter elephants from plantations in Peninsular Malaysia is the usage of electric fences and to promote tolerance towards elephants. These practices should be further encouraged. Other possible solutions that could increase human-elephant co-existence would require us to change our cultivation patterns and habits (crop types and methods). While we attempt to deter elephants from plantations, we could also employ designs that would attract them to habitats away from human-dominated landscapes.

Crop protection — Apart from electric fences, portable protection structures (e.g. thick wire mesh structures with lightweight rubber and repellent) can be explored to protect individual young trees below 7cm tree trunk diameter, and palms below 3m tall. As stems of most trees were broken around a height of 1m (max. 2.8m), it is likely that palms that the elephants feed on were not taller than 3—4m to canopy top. Comparative to the wild palms that elephants fed on, cultivated palms, *Elaeis guineensis*, around this height would be categorised as young palms (Miranda et al., 2019). Tree saplings that the elephants damaged were mostly less than 2cm diameter but can range up to 7cm. While the growth form of wild palms and the resprouting ability of tree saplings allow them to recover from herbivory damage in the wild (Bond and Midgley, 2001; Terborgh et al, unpubl.), the damage incurred would be different for cultivated plants. Unlike most wild species that are adapted to megafauna herbivory, trees such as rubber plants, *Heavea brasiliensis*, have barks that are easily peeled off in large pieces, potentially damaging the tree even when its latex serves as a deterrent. Young palms, and tree species whose bark are easily damaged (e.g. rubber and acacia) should not be planted near elephant habitats or could be protected to reduce potential damage by elephants.

Crop types — Native fruit trees such as the Santol fruit, *Sandoricum koetjape*, is likely to be able to resprout from elephant damage and can be cared for to allow them to recover following elephant damage. From camera traps directed at fruiting trees (e.g. *dillenia* spps.), no elephants were observed pushing over fruit trees although some branches were broken. Nonetheless, trees below 7cm diameter should be protected. Apart from artificial structures, trees can share a symbiotic relationship with insects such as ants, bees, or wasps, that elephants would avoid (King et al., 2007; Lev-Yadun & Ne'eman, 2012; Goheen & Palmer, 2010). Instead of treating insects as pests, they can be useful as small-scale elephant deterrents in farms. Studies can be carried out to explore more suitable fruit trees and protection methods for food crops. In BTFC, acacia trees were commonly planted along highways. The African bush elephants are known to feed on Acacia species (Okula & Sise, 1986). While this species can be fast-growing and may incur fewer damages as compared to oil palms, they potentially attract elephants to feed along highways. The overall effects of the Acacia plantations on wildlife can be further investigated.

Attracting elephants to their natural habitat — In addition to oil palm, rubber, and acacia plantations, grasses that grow in open habitats and along roads can also attract elephants to feed (English et al., 2014a; Wadey et al., 2018). While there is no solution to completely prevent elephants from entering these premises, wildlife corridors can be designed carefully with hotspots selected for restoration and tree-planting. On the downside, it may draw animals to these corridors to feed. On the bright side, it could allow elephants to remember and utilise these trails (Short, 1981; Vanleeuwé & Gautier-Hion, 2002; Blake & Inkamba-Nkulu, 2006) that would otherwise have been neglected or under-utilised. The species of plants or trees selected require more detailed planning. It would be appropriate to include factors such as the phenology of both wild and cultivated fruit trees, drought patterns, growth forms of grasses throughout the year, availability of riparian habitats, etc. into the establishments of the corridors.

Exploring the benefits of allowing elephants into plantations — The positive effects of allowing elephants into plantation grounds can be investigated to help promote tolerance towards elephants in plantations. In the plantation industry, both weed control and manuring are expensive operational costs to maintain (Nur Aida, 2019 cited Blair, 1980). Results from chapter 2 showed the impacts of elephants as large herbivores. The impacts, however, are not as destructive as they seemed. Instead, a combination of grazing, browsing, and manuring by elephants and other herbivores could help facilitate productivity through a positive feedback loop for nutrient availability in the system (Ruess, 1984; McNaughton and Chapin, 1985). In the shorter term, elephant damage can be a nuisance, but over longer-terms productivity may be richer in these elephant-utilised areas, reducing the need for costly weeding and the application of fertilisers that could leech and pollute our environment. Green manures have been successfully used in many agricultural practices (Tejada et al., 2008; Ayob & Kabul, 2009; Smithson & Giller, 2002). Along with this, nitrogen management may include legume rotations, and the inter-cropping of leguminous trees and shrubs (Smithson & Giller, 2002) to reduce fertilisation costs. This idea can be investigated with exclusion experiments in old oil palm plots, with and without elephants. Alternatively, remote sensing techniques such as the use of multispectral sensors may be explored to analyse oil palm stress factors and the need for fertilisers, and soil conditions between elephant utilized and non-utilized areas (Moreno et al., 2018).

Ethnobotany and Local Ecological Knowledge (LEK) — Linking phenology to the frugivorous community and investigating the seed dispersal network at a community level would not be possible without LEK in this study. The indigenous people have lived alongside Asian elephants for 55,000 years, sharing a considerable degree of coexistence in the landscape (Lim, 2020). As I highlighted the vulnerability of the actual system, I also highlighted the importance of sustaining LEK that is currently facing erosion in Belum-Temengor and Peninsular Malaysia. If no actions are taken to mitigate the erosion of LEK, I foresee a considerable decline with both LEK and biological sciences that depend on ethnobotanical or LEK knowledge over the next 20 years, alike the current scenarios in the Neotropical countries (Cámara-Leret et al., 2019). I encourage conscious efforts to preserve the original cultures and heritage of indigenous living.

I recognize the most urgent task for biological conservation concerning the LEK as 1) ensuring that the knowledge and skills continue to be passed on to the younger generations, 2) formalizing a para-taxonomy oriented education that could incorporate the indigenous people's way of learning while providing them with highly credited certifications, 3) recording accurate information concerning plant-animal interactions and, at the same time, 4) ensuring that the indigenous people get equitable sharing of benefits and stable income from the use of LEK. 5) We need to be careful that in the process of documenting LEK (including information added to the DNA library), local indigenous people will not be eventually excluded from long-term jobs while the information is readily made available. Actions for preserving LEK need to be incorporated formally to help indigenous communities secure stable incomes.

Increasing the Protection Status of Gibbons — Gibbons were the most efficient seed dispersers for plant species central to the network. Despite their dominance and importance as seed dispersers, they are currently endangered (IUCN, 2008). The gibbons are the preferred food of the local indigenous people (Kuchikura, 1988; Loke et al., 2020). While hunting of gibbons is constrained by the Wildlife Act, 1972 (Or & Leong, 2011) that disallowed gibbons to be hunted by indigenous people, illegal poaching by foreigners and non-indigenous people is still ongoing in forests like BTFC. Compared to the Malayan tigers and Asian elephants, gibbons have received less conservation attention in Peninsular Malaysia. Their protection should be considered a high priority

CONCLUSION

The Asian elephants are one of the last remaining megaherbivores in the Sundaic forests. They are highly interactive generalists that require a community or ecosystem approach to illuminate their ecological functions. In this Ph.D., I examined the ecological functions of Asian elephants in herbivory, frugivory, and seed dispersal, highlighting important interactions of elephants and the plant and animal communities. Unpublished studies that stemmed from this thesis include the monitoring of fruiting phenology and further elaboration of the consequences of defaunation.

In the closed canopy dipterocarp rainforest, the Asian elephants preferred monocots, especially palms as food. The availability of monocots in the forest, however, is low. Both palms and tree saplings formed the principal food of elephants. Their feeding behaviour could have resulted in a reduced density of palms in the Royal Belum rainforest, a forest with elephants, as compared to Krau, a forest where elephants were absent since 1993 (Terborgh et al., 2017). While elephants damage high numbers of tree saplings, these small stems had high recovery rates (Terborgh et al., unpubl.). Reduced tree sapling density in the Royal Belum could be the effect of both elephant herbivory and the collection of stems by wild boar for nest building (Ickes et al., 2003). More studies are needed to confirm the effects of stem breakage by both species on the dipterocarp forest structure. Although stem breaking by animals may appear destructive, this process can be important for enhancing the productivity of the dipterocarp forest, thereby increasing food availability to other herbivores. The indigenous practice of shifting agriculture creates small forest openings that provide good feeding grounds for herbivores. The interconnection of the Asian elephant, wild boars, and the indigenous people's practice on both forest structure and productivity can be further investigated.

Asian elephants are important for the dispersal of large-fruited species such as *Irvingia malayana*, which are uncommon in the forest. During the study period, *Irvingia malayana* mast-fruited with a large fruit crop that attracted both Asian elephants and wild boars to feed. Interestingly, elephants consumed only fresh fruits while wild boars foraged for older fruits. Seed dispersal by elephants allowed the *Irvingia malayana* to escape from efficient seed predation by the wild boars. The high germinability of elephant swallowed seeds also allowed the *Irvingia malayana* to be effectively dispersed.

In the seed dispersal network, Asian elephants disperse seeds of plants common to the community and also large-seeded species dispersed by seed hoarders such as rats. Their long-distance seed dispersal ability (Campos-Arceiz et al., 2008) and importance to enhancing seed germination (Torres et al., 2020) as compared to rats distinguish their dispersal prominence for large-seeded species. 22% (out of 164) of fruits collected had megafaunal syndrome traits (fruit width ≥ 40mm), of which the elephants dispersed 81% and rats hoarded 53% of the fruit species. The Asian elephants thus promote high variability and fitness to the seed dispersal community by being important seed dispersers for both central and large-fruited species.

Within the community, gibbons appeared as the most efficient and important seed disperser, and the Asian elephants are functional generalists. While both species promoted network redundancy, thus promoting network resilience to extinction, their roles cannot be substituted by another species. Apart from gibbons and Asian elephants, seed dispersers that contributed highly to network resilience include the binturong, civets (as a large taxonomic group), and sun bear. Animals belonging to different forest strata — hornbills (multi-species taxon), gibbons, Asian elephants, and rats (multi-species taxon) are important to network module organisation. The modules are connected by seed dispersers such as wild boars, hornbills, langurs, and macaques. The Belum seed dispersal network was not as resilient as it was presented as an intact network as several important seed dispersers are currently endangered or vulnerable (IUCN). Defaunation of highly connected seed dispersers reflected adverse cascading effects on seed dispersal functions. Urgent protection of gibbons and other important and vulnerable species such as binturong, the Asian elephant, the Malayan sun bear, several vulnerable hornbill species (refer Chapter four, Table 4.2), langurs, and the Malayan flying fox is needed.

A simple video of this study is shared in:
https://www.facebook.com/MEME.elephants/posts/2857736157649037

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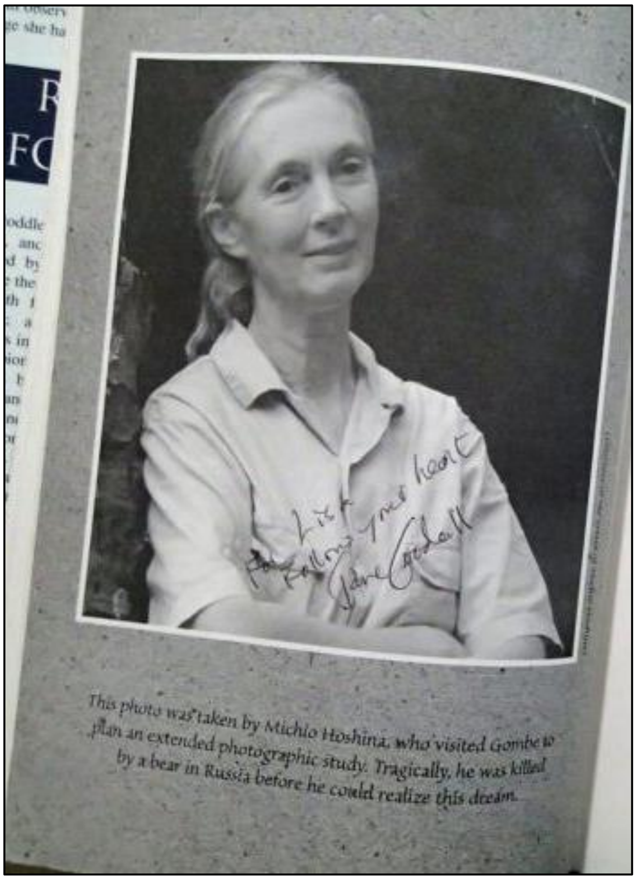

For Lisa
Follow your heart
Jane Goodall

This photo was taken by Michio Hoshina, who visited Gombe to plan an extended photographic study. Tragically, he was killed by a bear in Russia before he could realize this dream.

Follow your heart