Exploring Fruit-Frugivore Interactions and Post-Dispersal Seed Fate of Large-Seeded Plants in a Lowland Tropical Rainforest of Indonesian Borneo

by

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Dedication

To the children of the forest, who hold my heart.

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Abstract

Interactions between frugivores and the fruits they disperse play a crucial role in shaping plant population dynamics and ecosystem functioning. Large-bodied frugivores are particularly important as they are primary dispersers of fruits containing large seeds. Unfortunately, these frugivores are often preferentially targeted by hunters, and their loss can have profound effects on forest diversity, structure, and function. Despite the critical importance of understanding the ecological impacts of frugivore loss, many tropical regions lack community-level studies that assess region-specific patterns. Biodiverse Southeast Asian forests are facing significant challenges due to human-induced land-use changes and declining wildlife populations, especially among large-bodied species. Consequently, opportunities to study the vital relationships between diverse plants and frugivore species are rapidly diminishing. Comprehensive community-level assessments are imperative in the remaining areas that still retain diverse populations of large-bodied frugivores. The Cabang Panti Research Station in West Kalimantan, Indonesian Borneo, provides a unique opportunity for such research, as it has remained largely unaffected by anthropogenic influences. At this site, I characterized and evaluated fruit-frugivore interactions, specifically focusing on large-seeded plant species that depend on mutualistic interactions with large-bodied animals.

Chapter 2 of my study analyzes a network comprising 19 large-seeded liana and tree species and 25 interacting animal species. I assess interaction magnitudes, directions, and the impact of plant and animal traits on positive, neutral, and negative interactions. The results demonstrate a modular yet less nested (compared to networks in other SE Asia forests) frugivore-plant interaction network, showcasing a moderate level of specialization. Results show the differential impact of seed weight and animal body weight on the likelihood of positive and neutral interactions.

In Chapter 3, I examine post-dispersal seed fate for 15 large-seeded liana and tree species. My findings note that seeds placed farther from parents experienced lower predation rates, while seeds in high-density clusters under the canopy fared better than medium- and low-density clusters. Vertebrate seed predators, both large and small generalists, significantly affect seed mortality.

Chapter 4 represents the first multi-species assessment of hunting threats to 33 mammal and bird species that feed on fruits and seeds in Indonesian Borneo. My findings underscore that hunting disproportionately targets specific animal species in the region, potentially leading to the local extinction of at least one species, *Rusa unicolor*.

In summary, this study reveals a diverse frugivore and predator assemblage, emphasizing context-dependent interactions within fruit-frugivore and seed-predator networks. It also highlights a higher number of antagonistic interactions experienced by the studied plants compared to mutualistic interactions. Furthermore, some of the limited mutualistic interactions observed between the studied plants and large-bodied frugivores involve animals targeted by hunting.

Chapter 1: Introduction

1.1 Importance of fruit-frugivore interactions in tropical forests

The complex ecological interactions between frugivorous animals and plants that bear fleshy fruits constitute the primary mechanism of seed dispersal (Beckman et al., 2020; Jordano et al., 2011). In tropical forests, the majority (~80-90%) of woody plants produce fleshy fruits adapted for vertebrate consumption (Howe and Smallwood, 1982; Jordano, 1995). In these ecosystems, frugivores are ubiquitous, and both unripe and ripe fruits form key components of the diets of a wide range of vertebrate taxa (Corlett, 1998; Fleming and Kress, 2011).

Fruit-frugivore interactions involving seed-dispersing taxa are beneficial for both frugivores and plants. While frugivores gain nutritional benefits from consuming fruits (Garber and Lambert, 1998; Howe and Westley, 1988; Masi et al., 2015), frugivory benefits plants by dispersing their seeds, in turn affecting plant community diversity, structure, and functioning in numerous ways (Traveset and Richardson, 2014). Frugivores facilitate the movement of seeds to new areas. This process of spatial separation from the parent plant offers substantial advantages, allowing seeds to escape both intraspecific competition and the pressures imposed by specialized natural predators near conspecifics (Comita et al., 2014; Connell, 1971; Janzen, 1970).

Furthermore, frugivores remove fruit pulp and scarify seeds during gut passage, prior to releasing clean seeds, potentially enhancing seed germination (Rogers et al., 2021), particularly in the case of large seeds (Fuzessy et al., 2015 but see Verdú and Traveset, 2004). Additionally, frugivores disperse seeds at various distances and densities from parent plants, dependent on their ecology and behavior (McConkey et al., 2014; Morales et al., 2013; Russo et al., 2006). The wider the distribution of seeds, the higher the likelihood of seeds reaching diverse microsites, thereby increasing the probability of successful germination and establishment (García-Cervigón et al., 2018; Schupp and Jordano, 2010).

Fruit-frugivore interactions, particularly animal-mediated seed dispersal, increase the probability of plants colonizing new habitats (Howe and Smallwood, 1982; Nathan, 2006), are critical for plant species' persistence in disturbed habitats (Raoelinjanakolona et al., 2023; Razafindratsima et al., 2021), and enhance a plant species' capacity to adapt to climate change through range shifts (Fricke et al., 2022; Mokany et al., 2014). Further, animal-mediated seed dispersal, particularly through long-distance events, sustains gene flow and enhances genetic diversity within plant populations (Browne et al., 2018; Pérez-Méndez et al., 2016).

Finally, many plants that depend on animals for effective dispersal play a crucial role in providing a variety of provisioning and regulatory services to human communities, from supplying non-timber forest products to carbon storage (Bello et al., 2021; Egerer et al., 2017; García and Martínez, 2012). As a result, animals that consume fruits and disperse seeds, thereby sustaining plant population viability and diversity, are considered providers of essential ecosystem services (Egerer et al., 2017).

1.2 The role of large-bodied frugivores in the dispersal of large-seeded plants

Fruit-frugivore interactions display a high degree of complexity, involving a diverse spectrum of organisms ranging from small insects to large mammals (Farwig and Berens, 2012). The species most frequently recorded in these interactions encompass mammals, birds, and ants (Farwig and Berens, 2012). This diversity within frugivore assemblages encompasses animal species characterized by distinct traits and behaviors, belonging to different functional groups. Consequently, these frugivores interact with different fruit and seed types in a manner specific to their functional roles (Corlett, 2017), thereby contributing differently to the dispersal and establishment of plants (McConkey et al., 2018; Schupp et al., 2010).

Despite the wide variety of frugivores involved in interactions with fleshy-fruited plant species, the significance of large-bodied (>1 kg) frugivores such as elephants, ungulates, primates, fruit bats, and large birds within seed dispersal networks, especially in the case of large-seeded plants, has been extensively highlighted by several studies (Brodie et al., 2009; Campos-Arceiz and Blake, 2011; Corlett, 2017; Holbrook and Loiselle, 2009; Kitamura et al., 2006; McConkey and Drake, 2015; McConkey et al., 2018; Naniwadekar et al., 2019; Nunez-Iturri and Howe, 2007; Sethi and Howe, 2012). Large frugivores range over larger areas consuming a greater proportion of fruit (Holbrook and Loiselle, 2009; Jordano et al., 2007; Palacio et al., 2016). In addition, frugivores with larger body sizes possess greater gut capacity and longer gut retention times, allowing them to disperse seeds farther away than smaller animals (Campos-Arceiz and Blake, 2011; Mueller et al., 2014; Pires et al., 2018; Wotton and Kelly, 2012; but see Godínez-Alvarez et al., 2020).

Furthermore, fruit and seed traits may impose restrictions on access (Burns et al., 2013). For instance, small fruits or large, soft fruits with smaller seeds are accessible to and can potentially be dispersed by a diverse array of frugivores. However, large fruits with large seeds are predated by animals of various sizes (Babweteera et al., 2009) but can be effectively dispersed mainly by animals that can disperse seeds by swallowing them or carrying them (Ong et al., 2021). For example, while birds with small gapes are limited to dispersing small-sized seeds (Galetti et al., 2013), frugivorous hornbills with wider gapes can disperse a wide range of seeds, ranging from tiny *Ficus* (Kitamura et al., 2004) to large *Myristica* seeds (Kitamura and Poonswad, 2013; Kitamura et al., 2006). Additionally, smaller animals, such as seed-hoarding rodents, can disperse large seeds through synzoochory, which involves carrying seeds (Gómez et al., 2019).

Since large animals often occur at lower densities and are represented by fewer species in tropical rainforests (Babweteera et al., 2009; Vidal et al., 2013), large-seeded plants are likely dependent on a smaller number of mutualistic interactions (mostly but not exclusively) from large frugivores (Albert-Daviaud et al., 2022; Campos-Arceiz and Blake, 2011; Kitamura and Poonswad, 2013; Kitamura et al., 2006; McConkey et al., 2018; Naniwadekar et al., 2019; Ong et al., 2021; Sethi and Howe, 2012). These frugivores potentially offer non-redundant dispersal services that may not be compensated for by other taxa (McConkey et al., 2015; McConkey et al., 2018). Thus, given their importance within seed dispersal networks, extirpation or reductions in abundances of large-bodied frugivores may severely hamper seed dispersal, plant recruitment, and ecosystem functioning.

1.3 Large-bodied frugivores are some of the most threatened tropical forest taxa

Human-induced defaunation significantly contributes to the ongoing biodiversity crisis, particularly in tropical regions (Harrison et al., 2016; Ripple et al., 2016). Hunting poses a major threat to vertebrate populations, especially large-bodied animals, resulting in alarming declines in their biomass (Dirzo et al., 2014). These declines have significant implications for ecosystem processes.

The extirpation or decline of large-bodied animals providing unique ecological services, such as seed dispersal for large-seeded plants, are of particular concern (Terborgh, 2013).

Empirical evidence demonstrates that large-seeded, animal-dispersed plant species, experiencing fewer or no visits from remnant taxa, suffer decreases in sapling densities when large-bodied frugivores are absent or scarce, causing shifts in tropical forest structure characterized by lower species richness, increased clustering, and reduced diversity among animal-dispersed plant species (Brodie et al., 2009; Caughlin, 2015; Harrison, 2013; Kurten, 2013; Kurten et al., 2015; Markl et al., 2012; Nuñez-Iturri and Howe, 2007; Wright et al., 2007).

Furthermore, defaunation-induced shifts in plant communities could have significant implications for carbon storage potential of tropical forests (Bello et al., 2015; Chanthorn et al., 2019; Osuri et al., 2016; Poulsen et al., 2013; Peres et al., 2016). Studies suggest that defaunation results in reduced recruitment of heavy-wooded tree species, favoring small-seeded, fast-growing species. Consequently, disturbed landscapes, characterized by smaller-seeded communities, exhibit reduced maximum attainable height (Osuri and Sankaran, 2016). The decline of large tree species and reduced stand volumes remain the primary mechanisms for carbon loss in anthropogenic forested landscapes in the tropics (Osuri et al., 2016). However, the impact of defaunation on carbon storage varies regionally (Osuri et al., 2016), with inconsistent evidence (Harrison et al., 2013; Williams and Brodie, 2023), necessitating further exploration. Additionally, given the slow growth of tropical plants and the time lag in their response to hunting, the full extent of the impact of hunting on biomass and ecosystem functions may not have fully materialized yet, and several zoochorous plant species may be accumulating an eventual "extinction debt" (Brodie et al., 2009).

1.4 Framework and summary of chapters

In summary, fruit-frugivore interactions are pivotal for plant population dynamics and long-term adaptability in the face of environmental change (Corlett and Westcott, 2013; McConkey et al., 2012). Understanding the structure of diverse animal communities involved in such interactions is crucial for assessing ecosystem resilience against human-induced disturbances (Fricke et al., 2018; García et al., 2013). Large-bodied frugivores, most often at risk from defaunation, play vital roles in such interactions (Albert-Daviaud et al., 2022; Bogoni et al., 2020; Kitamura and Poonswad, 2013; Naniwadekar et al., 2019; Ong et al., 2021, 2022; Osuri et al., 2020; Wen et al., 2020), yet comprehensive assessments of their contributions are lacking from many tropical regions (Vidal et al., 2013). This underscores the need for more community-level studies to identify region-specific patterns, imperative to evaluate the consequences of frugivore loss on ecosystem dynamics (Albert-Daviaud et al., 2022).

The need for such assessments is particularly pressing in Southeast Asian forests, which are renowned for their high faunal and floral biodiversity, supra-annual fruiting patterns, and diverse frugivore assemblages (Corlett, 2007; Corlett, 2017). Yet, there are very few community-level studies on fruit-frugivore interactions from such forests (Albert-Daviaud et al., 2022; Brodie et al., 2009; Ong et al., 2022). Furthermore, as Southeast Asian forests continue to face severe threats from human-driven land-use changes and the accelerated declines of large-bodied frugivores due to defaunation (Harrison et al., 2016), opportunities to study the full suite of complex interactions between diverse plant and frugivore species at the community level are rapidly declining. Therefore, it is imperative and urgent that comprehensive community-level assessments are conducted in the few areas that still retain relatively higher diversity and abundances of large-bodied animals.

This dissertation focuses on the study of interactions large-seeded plant species and fruit- and seed-eating taxa. The research was conducted at the Cabang Panti Research Station, situated within the Gunung Palung National Park (GPNP) in West Kalimantan, Indonesian Borneo. GPNP is a tropical lowland rainforest site that has remained largely untouched by anthropogenic influences and still retains a diverse vertebrate and plant assemblage. The primary objectives of this research were to identify frugivore and seed predator assemblages, construct seed-disperser and seed-predator networks, and assess the significance of large-bodied animals for large-seeded plant species. Furthermore, we assessed threats from hunting to large-bodied frugivores in human modified landscapes adjacent to GPNP.

Chapter 2: Large-Bodied Frugivores: Critical Mutualists within Fruit-Frugivore Interaction Networks of Large-Seeded Plant Species in a Bornean Lowland Rainforest. Fruit-frugivore interactions are often complex, involving multiple animals and plants with distinctive behaviors and traits. These interactions can be represented using interaction networks, which enable us to understand community structure, the robustness of networks to perturbations, and the functional importance of each species within networks (Carlo and Yang, 2011). In this chapter we evaluated visitation rates, quantity of fruit removal, and nature of frugivory (fruit/seed handling behavior) at large-seeded plant species through 1439.2 hours of fruit plant observations at 37 individual large-seeded trees and lianas belonging to 19 species. The observational data were then utilized to describe a bipartite (two-part, i.e., plants and animals) fruit-frugivore network and examine the roles of different animal species.

Chapter 3: To Eat or to Move: Investigating Mutualistic and Non-Mutualistic Interactions Within a Seed Predator Network in a Lowland Rainforest in Indonesian Borneo. In this chapter, we conducted an experimental assessment of post-dispersal seed fate for large-seeded plant species. A diverse array of seed predators is known to interact with seeds dispersed by frugivores. These interactions are influenced by many factors such as resource availability, seed traits, and the biology of the predators themselves, and have a significant impact on seed mortality and establishment (Lichti et al., 2017), highlighting the need to evaluate the collective influence of multispecies interactions on plant reproductive success. Over a span of 13 months, we closely monitored the fate of 963 tagged seeds. These seeds belonged to 20 large-seeded tropical rainforest plants, representing 15 different species. We strategically placed these seeds at varying densities and distances from the parent plants. We employed camera traps and conducted periodic visits to observe and record the outcomes. This study meticulously documented seed predator assemblages, evaluated seed-predator interactions, and examined how different predators responded to various factors, including seed density, proximity to parent plants, and seed traits.

Chapter 4: Contemporary Hunting Practices in a Forest-Plantation Mosaic Landscape in West Kalimantan, Borneo, Indonesia. This chapter focuses on assessing the threats posed to large-bodied frugivores by hunting within anthropogenically modified landscapes. Gunung Palung National Park (GPNP) is largely unaffected by anthropogenic disturbance and consequently stands as an anomaly within the landscape. Areas outside the national park have experienced significant transformation, resulting in what is now best described as a mosaic of forests and plantations. Such transformation potentially results in increased human access to the remaining forest patches and their resources (Harrison et al., 2016; Benítez-López et al., 2019). Within these contemporary landscapes, we conducted a systematic, multi-species assessment of hunting, with a particular focus on 33 species of large-bodied mammals and birds that incorporate fruit to varying extents in their diet. To achieve this, we employed a three-part structured questionnaire administered to 29 willing Muslim Melayu hunters residing in villages adjacent to GPNP. Our objective was to identify frugivorous species most threatened by hunting, quantitatively analyze the scale and motivations for hunting, and assess current perceptions toward hunting.

In **Chapter 5**, the concluding chapter, I contextualize the results of each chapter, placing my work in a broader context and highlighting priorities for future work.

In summary, my research highlights a diverse frugivore and predator community. It underscores that interactions within fruit-frugivore and seed-predator networks are context-dependent, with their direction and magnitude varying across animal and plant species that differ in traits. Importantly, my research highlights the limited number of mutualistic interactions between the plants under study and frugivores, that include vertebrates disproportionately targeted by hunting.

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Chapter 2: Large-Bodied Frugivores: Critical Mutualists within Interaction Networks of Large-Seeded Plant Species in a Bornean Lowland Rainforest

2.1 Abstract

Studying fruit-frugivore networks in diverse tropical ecosystems is complex yet crucial, especially amid the widespread decline of large-bodied animals, including frugivores, and the risk of losing irreplaceable mutualistic interactions. Over a 15-month period, we conducted a comprehensive study in the lowland tropical rainforest of Indonesian Borneo. Our focus was on interactions between frugivores and large-seeded plants (seed length >15 mm). The objectives of our study were to evaluate various types of interactions between these plants and their animal visitors, assess the structure of the fruit-frugivore network using both species-level and network-level metrics, and investigate the impact of fruit, seed, and animal traits on mutualistic interactions. We collected data on interactions between plants and animals during 1,439.2 hours of fruit-tree watches and through remotely triggered camera traps. A total of 789 fruit/seed handling interactions were observed and used to characterize the fruit-frugivore network. This network encompassed 19 species of large-seeded lianas and trees, and 25 animal species and groups. Our findings revealed a modular yet less nested (compared to networks in other SE Asia forests) fruit-frugivore network with a moderate level of specialization. It featured specialization among some frugivores, generality among many others, and relatively limited overall connectivity, resulting in uneven interaction distribution among species.

Furthermore, our results emphasized the influence of seed weight and animal size on positive and neutral interactions (combined), highlighting the disproportionately significant role of larger animals in these interactions. Large-seeded plants primarily experienced more antagonistic interactions than mutualistic ones, with large-bodied animals driving both types. Importantly, several key large-bodied mutualists and antagonists in this network are currently classified as Endangered, Vulnerable, and Near Threatened (IUCN, 2022).

2.2 Introduction

In tropical forests, many animals visit and interact with fruiting trees. These interactions can be mutualistic (such as seed dispersal), antagonistic (such as seed predation), or neutral (such as pulp-pecking), or a combination of them (Simmons et al., 2018). The net outcome of the type and frequency of these interactions profoundly influences plant reproductive success (Simmons et al., 2018).

For sessile organisms like plants, mutualistic interactions such as seed dispersal play a pivotal role in maintaining species diversity (Nathan and Muller-Landau, 2000; Terborgh, 2013). Approximately 80-90% of tropical plant species rely on frugivores for seed dispersal (Howe and Smallwood 1981; Jordano 1995). Seed dispersal offers several advantages to plants: it allows them to escape predators, parasites, and pathogens at the natal site (Comita et al., 2014; Connell, 1971; Janzen, 1970), increasing their chances of reaching sites more conducive to germination (García-Cervigón et al., 2018; Schupp and Jordano, 2010); enables them to colonize unoccupied habitats (Howe and Smallwood, 1982; Nathan, 2006); facilitates the expansion of their geographic ranges (Fricke et al., 2022; Mokany et al., 2014); and helps maintain genetic diversity in plant populations (Browne et al., 2018; Pérez-Méndez et al., 2016).

2.2.1 Large-bodied mutualists do matter

In tropical forests interactions between fruiting plants and animal visitors display a high degree of complexity (Bascompte and Jordano, 2007; Donatti et al., 2011). These interactions involve a diverse spectrum of organisms, ranging from small insects to large mammals (Farwig and Berens, 2012). Despite this diversity, several studies have emphasized the significance of large frugivores (>1 kg), such as elephants, ungulates, primates, fruit bats, and large birds, within seed dispersal networks (Brodie et al., 2009; Campos-Arceiz and Blake, 2011; Corlett, 2017; Holbrook and Loiselle, 2009; Kitamura et al., 2006; McConkey and Drake, 2015; McConkey et al., 2018; Naniwadekar et al., 2019; Nunez-Iturri and Howe, 2007; Sethi and Howe, 2012).

The role of large frugivores becomes particularly crucial in the context of large-seeded plants. While small fruits or large, soft fruits with smaller seeds can be accessible to and potentially dispersed by a diverse array of fruit and seed eating taxa, large-seeded fruits, although subject to predation by many animals (Babweteera et al., 2009), are primarily, though not exclusively, dispersed by large frugivores capable of swallowing or carrying seeds (Galetti et al., 2013; Gómez et al., 2019; Kitamura and Poonswad, 2013; Kitamura et al., 2006; Kitamura et al., 2004; Ong et al., 2021b).

Moreover, larger frugivores cover larger areas and consume a greater proportion of fruit (Holbrook and Loiselle, 2009; Jordano et al., 2007; Palacio et al., 2016). Their larger body sizes provide greater gut capacity and longer gut retention times, enabling them to disperse seeds over longer distances compared to smaller animals (Campos-Arceiz and Blake, 2011; Mueller et al., 2014; Pires et al., 2018; Wotton and Kelly, 2012 but see Godínez-Alvarez et al., 2020). To add, large frugivores are often found at lower densities and are represented by fewer species in tropical rainforests (Babweteera et al., 2009; Vidal et al., 2013). Consequently, large-seeded plants rely on a smaller number of mutualistic interactions, primarily, though not exclusively, involving large frugivores (Albert-Daviaud et al., 2022; Campos-Arceiz and Blake, 2011; Kitamura and Poonswad, 2013; Kitamura et al., 2006; McConkey et al., 2022; McConkey et al., 2018; Naniwadekar et al., 2019; Ong et al., 2021a,b; Qie et al., 2019; Sethi and Howe, 2012). These interactions may provide non-redundant dispersal services (McConkey et al., 2022; Qie et al., 2019).

While the role of large frugivores, especially in long-distance dispersal, is undisputed (McConkey and Drake 2015; Sridhara et al., 2016), recent studies continue to shed light on the role of smaller-bodied species, such as rats, in dispersing large seeds through non-zoochorous methods, for e.g. transporting seeds to caches (Carreira et al., 2020; Ong et al., 2021b). Therefore, to identify crucial seed dispersal roles and understand the importance of body size, it's essential to assess diverse ecological networks encompassing a wide range of body sizes, seed-handling behaviors, and dietary preferences.

2.2.2 Unraveling the role of large-bodied animals in networks of large-seeded plants

Despite their vital role in seed dispersal networks, large frugivores are often excluded from community-wide assessments of interactions between fruiting plants and animal visitors. This omission results from a limited focus on specific functional guilds with a narrower range in body size, such as birds, and the fact that many regions where such assessments have occurred have witnessed extensive extirpations of large animals (Vidal et al., 2013). Consequently, to understand region-specific patterns and grasp the implications of frugivore loss on plant dynamics, conducting community-level studies is imperative in the few regions that still support diverse frugivore assemblages (Albert-Daviaud et al., 2022).

While studying interactions in hyper-diverse communities is challenging, employing a network approach offers a means to unravel the complexity within such systems (Bascompte and Jordano, 2007; Ings et al., 2009). Analyzing ecological networks and their structure helps us quantitatively assess the relative roles of a broad range of participating species at the species level and the robustness of the network to perturbations at the community level simultaneously (Carlo and Yang, 2011).

In studying mutualistic networks, recurrent structural patterns have been observed (Bascompte and Jordano, 2007). Studies on plant-frugivore networks have demonstrated nestedness (Albert-Daviaud et al., 2022; Bascompte et al., 2003; Ong et al., 2021a,b), where generalists interact with most species, while specialists have interactions mainly with generalists. This feature is thought to enhance a community's resilience to species loss (Bastolla et al., 2009; Thébault and Fontaine, 2010), as generalists interacting with many partners are robust to extinctions. This ensures critical functions can be maintained even if some species are lost and influences patterns of trait evolution (Bascompte and Jordano, 2007).

Mutualistic networks have also been observed to be modular (Albert-Daviaud et al., 2022; Bascompte and Jordano, 2007; Naniwadekar et al., 2019; Ong et al., 2021a,b), where species form subsets or modules interacting more with each other than with those in other modules within the network (Donatti et al., 2011; Thébault, 2013). The modular structure in networks implies high functional diversity, which enhances the robustness of the network to perturbations, as weak links between modules slow the spread of perturbations between modules (Kolchinsky et al., 2015). Therefore, richer modular communities are more likely to persist in the face of anthropogenic challenges (Ramos-Robles et al., 2020).

In this study, we analyze a network involving large-seeded plants (>15 mm seed length) and a diverse community of fruit and seed-eating species, ranging in size from small rodents to large Bornean orangutans and bearded pigs. We examine the network's composition and structure using both species-level and network-level metrics. Additionally, we assess the proportions of mutualistic to non-mutualistic interactions between animal visitors and plant species and identify important mutualists. Finally, we investigate the influence of fruit, seed, and animal traits on the likelihood of mutualistic interactions.

2.3 Methods

We collected data over 15 months: in June and July of 2016, in June 2019, from November 2019 to May 2020, and from August to December 2020. Our study was conducted during the inter-mast period. Most forest types in our ecosystem are characterized by frequent and prolonged periods of low fruit production between mast fruiting events (Marshall et al., 2009) and no discernible annual pattern in fruit phenology (Cannon et al., 2007). Given this uncertainty in fruit availability, we could not preselect large-seeded plant species for our study. Instead, we included individuals and species based on availability during the study period.

2.3.1 Field methods

To locate plants bearing fruit, we walked along existing trails and searched select locations off trails, thoroughly scanning the canopy and the forest floor for fruits and seeds. We also relied on sounds of animal activity to locate fruiting plants, especially those with large fruits (specifically *Canarium* sp. and *Willughbeia* sp.) that were clearly audible when they fell to the forest floor. Finally, we frequently checked in with other researchers working at the research site for information on the location of fruiting plants (e.g., inside long-term phenology plots). Focal plant individuals were separated from each other in space and/or time, each monitored plant stem was at least 100m from any other monitored stem that was producing fruit concurrently, with one exception when one individual of *Diospyros* sp., *Willughbeia* sp. *1*, and *Palaquium sp*. each were fruiting at the same time within 100m of one another.

Direct observations of interactions between fruiting plants and animal visitors: We assessed interactions through direct observations at fruiting plants, conducting continuous watches for varying durations of time between dawn and dusk, specifically from 0600 to 1730 hrs. Each fruit plant watch began with the categorization of fruit crop size into specified ranges, which included less than 25, 25-50, 50-100, 100-250, 250-500, 500-1000, and 1000-2500 fruits. During each fruit plant watch we recorded the following observations: (a) identity of visitor, (b) number of individuals, (c) entry and exit time, (d) start and end of fruit/seed eating bouts, which sometimes coincided with entry and exit times, (e) fruit/seed handling behavior, and (f) fruit removal rate, encompassing the number of fruits ingested, dropped, or carried away.

Each animal visit was classified as a feeding bout when fruit and/or seed handling were noted, else it was classified as a non-feeding bout.

During feeding bouts, fruit and seed handling behaviors, were categorized into distinct types, such as whole fruit swallowing (including both pulp and seeds), carrying away whole or partially eaten fruits, carrying away intact seeds with or without pulp, consuming pulp while dropping or spitting out intact seeds, dropping whole or partially eaten fruits with intact seeds, seed predation, feeding on fallen fruits/seeds, and feeding on fruit while still attached to the parent plant (in situ). Under each of the fruit/seed handling categories, we assigned a value of '1' when the behavior was observed during a visit, and '0' when that behavior wasn't observed.

We made every effort to note the number of seeds removed; however, it's important to note that this was not feasible for multi-seeded fruits with varying seed counts.

Indirect observations of interactions between fruiting plants and animal visitors: We placed one camera trap (Bushnell 16MP Trophy Cam HD Essential E3 Trail Camera) at each fruit plant to monitor terrestrial frugivory behavior by elusive and shy diurnal as well as nocturnal visitors (Prasad et al., 2010). The cameras were configured to record videos lasting 20 seconds with a delay time of 1 second between recordings. We extracted key data from the videos, including visitor identity, the number of individuals, entry and exit times (with respect to the camera's field of view), the start and end times of fruit/seed eating, and fruit/seed handling behavior.

The fruit and seed handling behaviors were noted under the following categories, whole fruit swallowing (including both pulp and seeds), carrying away whole or partially eaten fruits, carrying away intact seeds with or without pulp, consuming pulp while dropping or spitting out intact seeds, dropping partially eaten fruit with intact seeds, and seed predation. Under each of the fruit/seed handling categories, we assigned a value of '1' when the behavior was observed during a visit, and '0' when that behavior wasn't observed.

Fruit traits: We measured fruit and seed traits from 5 to 64 mature (per species), undamaged fruits that were gathered from the forest floor. These fruits belonged to 27 individual plants belonging to 18 different species and 11 distinct families (see Table A2.1 for details). Unfortunately, we couldn't obtain trait information for the *Hydnocarpus* species because no intact fallen fruits or seeds could be located.

Once we had collected the fruits, we transported them to our research station's laboratory. Here, we cleaned the fruit without damaging the fruit coat. Subsequently, we recorded the following information:

(a) fruit shape, categorized as either globose, ovoid, ellipsoid, or other,

(b) fruit coat color noted as yellow, orange, red, violet, brown, or green following Gautier-Hion et al., 1985,

(c) fruit weight in grams, measured using a Fristaden Lab Digital Precision Analytical Balance Lab Scale (with a 1000g x 0.01g scale and 0.01g accuracy),

(d) fruit dimensions, including length (longest axis) and width (second longest axis), measured using a Mitutoyo high-precision digital caliper,

(e) fruit scent, classified as strong, mild, or undetectable based on our perception,

(f) fruit protection, categorized into three types: skin that can be pierced by a fingernail, thick skin or rind (e.g., similar to oranges), and a hard fruit wall that cannot be easily removed (following Gautier-Hion et al., 1985),

(g) thickness of fruit protection, measured using a Mitutoyo high-precision digital caliper,

(h) pulp type, with the following options: juicy soft, juicy fibrous, dry soft, dry fibrous, and only the seed being edible (based on Gautier-Hion et al., 1985),

(i) weight of edible tissue,

(j) ratio of edible tissue weight to total seed weight, and

(k) total number of seeds.

Additionally, for a subset of seeds, we conducted measurements of their length, width, thickness, and weight using a Mitutoyo high-precision digital caliper and a Fristaden Lab Digital Precision Analytical Balance Lab Scale (with a 1000g x 0.01g scale and 0.01g accuracy). For seed protection, we categorized each species as 'soft' (capable of being broken by a fingernail), 'hard' (resistant to breakage by fingernail), or 'stone' (seeds with true stones).

2.3.2 Analytical methods

We used the R statistical and programming environment for data analysis and visualization (R Core Team, 2021).

Following Simmons et al., (2018), we characterized the different types of interactions and their direction from the plant's perspective by categorizing recorded fruit and seed handling behaviors as follows: positive—swallowing whole fruit or pulp and seeds, and carrying away whole or partially eaten fruits; neutral—consuming pulp while dropping or spitting out intact seeds under the parent plant, dropping whole or partially eaten fruit under the parent plant, and feeding on fruit while still attached to the parent plant (in situ); and negative—carrying away intact seeds, and/or feeding on seeds.

Subsequently, we computed both counts and proportions of positive, neutral, and negative interactions separately for animal and plant species. When proportions of positive and negative interactions equaled or exceeded 0.5 of total interactions for a species, it was noted as an important mutualist or predator, respectively.

We visualized interactions between seed predators and individual plant species through a bipartite network diagram. The network diagram's construction was based on the total number of feeding bouts recorded between each animal and plant species. This accounted for feeding visit frequency but did not encompass data on frequency of different interaction types (i.e., positive, neutral, or negative). We were unable to identify rats at the genus and species level; therefore, they were categorized under the category 'rats.' Similarly, all species of small *Callosciurus* squirrels were placed under the category 'small squirrel species'.

To create this diagram, we utilized the plotweb() and visweb() functions from the {bipartite} package (Dormann et al., 2008).

Our network analysis consisted of two levels: network-level and species-level. At the network level, we calculated metrics such as Weighted Nestedness Overlap and Decreasing Fill (Weighted NODF), Specialization (H_2), and Weighted Connectance (C) using the networklevel() function (Simmons et al., 2018).

Weighted NODF measures the organization of network interactions on a scale from 0 to 100. In networks with high Weighted NODF (closer to 100), interactions are highly structured, and some species act as generalists, engaging with a wide range of other species. This redundancy contributes to the network's overall robustness.

Specialization, as measured by the H_2 index, ranges from 0 to 1 and informs us about the degree of specialization or generality exhibited by species within the network. High specialization (closer to 1) suggests that species interact with only a few others, while low specialization (closer to 0) means they interact with many different species.

Weighted Connectance (C), which also ranges from 0 to 1, serves as a measure of network connectivity. It reflects the proportion of possible interactions that are realized in the network. A value of 0 indicates no connections or interactions, while a value of 1 indicates that all possible interactions between the species on both axes (e.g., plants and animals in this case) are realized. Weighted Connectance considers interaction strength, revealing how much of the potential interaction strength in the network is observed. Higher C values indicate a denser network with more realized interactions. While these are general guidelines, interpretation can vary with ecological context.

At the species level, we computed metrics such as degree and strength using the specicieslevel() function. Degree represents the number of plant species each seed predator interacts with, giving insight into the diversity of partners each predator engages with. Strength, on the other hand, captures the level of interdependence within the network. Interaction strength (bij) quantifies the proportion of a species's interactions with a specific partner (species j) relative to its total recorded interactions (Bascompte et al., 2006).

To identify distinct modules within the network, we applied the Louvain algorithm, which is designed for detecting clusters in bipartite networks (Blondel et al., 2008). We ran the algorithm 50 times to compute modules (Donatti et al., 2011) and selected the composition with the highest modularity, following the approach employed in other network analysis studies (Naniwadekar et al., 2019; Ong et al., 2021a). Modules refer to groups of nodes (or entities) within a network that are more tightly connected to each other than to nodes outside the group. They help identify clusters or communities of related elements within a larger network, aiding in the understanding of the network's structure and organization. These network modules were visualized using the {igraph} package (Csardi and Nepusz, 2006; Csárdi et al., 2023). Modules were visualized both together and separately. In the individual module plots, animal species nodes were weighted and sized based on the number of interactions. These visualizations were created using the plot() function from the {igraph} package.

Finally, we employed a parametric approach to assess the influence of fruit and seed traits, including fruit weight, fruit length, fruit skin width, pulp weight, total seed weight, pulp-seed ratio, total number of seeds, seed weight, seed length, and seed protection, as well as animal body weight on the proportion of positive and neutral interactions (combined i.e., (positive+neutral)/(positive+neutral+negative)).

To explore the influence of predictors on the response variable, we utilized linear mixed-effects models with the 'lmer()' function from the 'lme4' package (Bates et al., 2015), using the Restricted Maximum Likelihood method for model fitting. All continuous predictors were standardized and centered around the mean before their inclusion in the model. The models included single predictors and combinations of animal body mass with each of the fruit or seed trait variables, both as fixed effects and as two-way interactions (see Table A2.3). Additionally, we added plant ID as a random effect to account for pseudo-replication since each tree was sampled multiple times.

Model comparison was conducted using Akaike's Information Criterion corrected for sample size (AICc) with the 'AICctab()' function from the 'bbmle' package (R Core Team, 2021). To facilitate interpretation, we back-transformed (exponentiated) both beta coefficients and the confidence interval boundaries from the log scale to the original scale. This allowed us to obtain predicted probabilities that are more intuitive and easier to interpret.

2.4 Results

We completed a total of 156 fruit tree watches, encompassing 37 individual trees and lianas from 19 plant species and 12 plant families (refer to Table A2.1).

On average, each fruit plant watch lasted 9.4 hours (MIN=2; MAX=11.3; SD=2.3), resulting in a cumulative total of 1459.1 hours of fruit watches. On 33 occasions, plant watches were temporarily halted due to heavy rain, accounting for 19.9 hours of watches (AVG=0.6; SD=0.3; MIN=0.1; MAX=1.4). Therefore, our total sampling effort for this study was 1439.2 hours.

On ten sampling occasions (days), accounting for 91 hours, no visitations were observed. A total of 1741 visits were recorded from fruit plant watches, camera traps, and an opportunistic record of frugivory by a sun bear. Visits were considered independent if visitors exited the tree or the field of view of the camera trap for more than fifteen minutes. Of the recorded visits, 789 were feeding bouts (Figure A2.1). Accidentally dropping fruit while moving across the tree was not included among these interactions.

The remaining 952 non-feeding bouts constituted other behaviors including searching (n=379), inactive (n=94), passing through, under or next to focal plants (n=494) among others (n=99) (Figure A2.1). They are not included in the subsequent analyses.

2.4.1. Interactions between animal visitors and large-seeded plants

During 789 feeding bouts, we recorded twenty-five animal species and groups, encompassing a minimum of 28 species (Table 2.1), that interacted with the nineteen focal plants, and the number of interactions between animal species/groups and plant species ranged from a minimum of 0 to a maximum of 216 (Figure 2.1). A total of 151 positive, 566 neutral, and 425 negative interactions were observed (Table 2.2; Figures 2.2 and 2.3).

Out of 151 positive interactions, 105 (65.5%) involved nine species of large frugivores (>1 kg). The remaining 30.5% (n=46) involved a minimum of 3 small squirrel species, with Prevost's squirrel being responsible for 87% (of 46) of these interactions. Among the neutral interactions, 51.9% (n=294) involved 13 species of large animals, while 48.1% (n=272) involved 2 species of small squirrels, with Prevost's squirrel contributing to 79.4% (of 272) of these interactions. In the case of negative interactions, 76% (n=323) were linked to 14 species of large animals, while 24% (n=102) were attributed to 5 species of small animals. Among these, rats were responsible for 50% (of 102) of the interactions, while three-striped ground squirrels accounted for 31.4% (of 102).

With respect to plants, the following species experienced zero positive interactions: *Willughbeia* sp. 4, *Parartocarpus* sp., *Palaquium* sp., *Irvingia malayana*, and *Hydnocarpus* sp. (Figures 2.3 and 2.4). With respect to animals, positive interactions were noted only in the case of a) muntjacs that swallowed whole fruit (n=29), b) Bornean white-bearded gibbons (n=39), Bornean orangutans (n=14), binturongs (n=3), palm civets (n=14), and a sun bear (n=1) that swallowed pulp and seeds, and c) southern pig-tailed (n=1) and long-tailed macaques (n=3), pale giant (n=1), Prevost's (n=40), three-striped ground (n=1), and small *Callosciurus* (n=5) squirrels that carried away whole and/or partially eaten fruits. However, for red langurs, bearded pigs, mouse deer, yellow-throated martens, long-tailed, thick-spined, and Malayan porcupines, tufted ground squirrels, rats, Malay and banded civets, Bornean crested firebacks and emerald doves, zero positive interactions were recorded (Table 2.2; Figures 2.2 and 2.3).

Sun bears, muntjacs, and Bornean white-bearded gibbons were noted as key mutualists, showing ≥ 0.5 proportion of positive interactions (of all interactions observed for each of these species) (Table 2.2). Conversely, bearded pigs, southern pig-tailed macaques, mouse deer, banded and Malay civets, tufted ground squirrels, three-striped ground squirrel, all species of porcupines, rats, Bornean crested firebacks, and emerald doves were noted as key predators, showing ≥ 0.5 proportion of negative interactions (Table 2.2). Additionally, Bornean orangutans, red langurs, binturongs, long-tailed macaques, palm civets, yellow-throated martens, and pale giant, Prevost's, and small Callosciurus squirrels all showed ≥ 0.5 proportion of neutral interactions (of all interactions observed for each of these species) (Table 2.2).

2.4.2. Interaction network

In this network analysis, an interaction signifies a feeding bout, as the frequency of these feeding bouts was employed to characterize our network. In the bipartite network (Figure 2.4; Table 2.3), the degree index, representing the number of links, indicates the number of plant species that animal visitors interact with. Pigs were connected to 13 plant species, Prevost's squirrels had 12 links, and both Bornean orangutans and long-tailed macaques had 10 links each (Figure 2.4; Table 2.3). On the plant axis, *Madhuca* sp. and *Lansium domesticum* were linked to 12 and 11 animal species, respectively, while *Dracontomelon costatum* and *Willughbeia* sp. 1 and 3 each had 10 links (Figure 2.4; Table 2.4).

The width of a link signifies the strength index, a weighted metric based on the relative frequency of interactions between the linked animal and plant species. Among the animal species, associations of pigs (with greater proportion of negative interactions as noted in the preceding section), and Prevosts's squirrels (with a high proportion of neutral interactions) with their plant species were notably stronger when compared to other predators, with a strength index of 3.1 and 2.7 respectively (Figure 2.4; Table 2.3). It's important to note that rats and small squirrel species encompass groups with multiple species. As a result, it is probable that the species within these groups have a reduced level of representation at the species level if all taxa could have been identified to species.

A Weighted NODF of 20.88 suggests a relatively low level of weighted nestedness in this network. This implies that the interactions in this network are less structured, and specialists with highly specific interactions may be more common.

Specialization (H_2), a metric that quantifies the degree to which animals in the network are specialized in their interactions with plants ranging between 0 and 1, showed a value of 0.39

suggesting that, on average, the animals in this network exhibit a moderate level of specialization. This means that while some frugivores may have highly specific preferences for certain types of plants, others are more generalist in their interactions.

Weighted Connectance (C), a measure of how connected the interactions are within the network, considering both the number of interactions and the strength of those interactions ranging from 0 to 1, showed a value of 0.13 indicating that the network was relatively less connected. In other words, not all frugivores interact with all available plants, and the interactions between frugivores and plants may be sparse or less intense.

The best composition selected based on the optimization process showed that the interaction network consisted of five modules, as illustrated in Figure 2.5, with a modularity value of 0.296 (p-value: 0.023). Module 1 included four plant species and six animal species (Figure 2.5). Among the plants, *Madhuca* sp. was linked to all six animal species in this module, and among the animals, the highest number of feeding interactions was observed among long-tailed macaques in this module (Figure 2.5).

Module 2 comprised four plant and six animal species, with *Strychnos* sp.2 and sp.1 among the plants, attracting a greater diversity of animal species (n=6 for sp. 2 and n=5 for sp. 1, respectively). Among the animals, red langurs and rats interacted with all four plant species in the module, and the highest number of feeding interactions was noted for red langurs, followed by rats (Figure 2.5). Module 3 represented the least diverse module, consisting of two plant species and three animal species, with the highest number of feeding interactions recorded for the small *Callosciurus* species, followed by mouse deer (Figure 2.5).

Module 4 featured six plant species, with *Willughbeia* sp. 1 drawing a greater diversity of animal species (n=5; Figure 2.5). Within this module, six animal species were present, with

Bornean orangutans and Prevost’s squirrels interacting with the most plant species (n=5 each). Prevost’s squirrels had the highest number of feeding interactions.

Finally, module 5 comprised three plant species, all with single-seeded stony seed protection. In this module, all three animal species interacted with *Canarium* sp.1. The tufted ground squirrel and pale giant squirrel interacted with all three plant species. Seed-dispersing muntjacs, followed by the specialized seed predator tufted ground squirrels, had the highest number of feeding interactions (Figure 2.5).

2.4.3 Influence of functional traits on positive and neutral interactions (combined)

Among the 41 linear mixed-effects models that we compared, the model incorporating seed weight, animal weight, and their interaction emerged as the top-performing model, holding 72% of the Akaike weight (Table A2.2). The results suggest that, when animal body weight is held constant, a one-unit increase in seed weight leads to an increased likelihood of a positive or neutral interaction event by 1.07 (SE = 1.07; 95% CI = 0.94-1.22) (Figure 2.6). However, it's important to note that this effect is less reliable, as the confidence interval overlaps with the no-effect line. In contrast, when seed weight is held constant, a one-unit increase in animal body weight reliably decreases the odds of a positive to neutral interaction event by 0.80 (SE = 1.03; 95% CI = 0.76-0.85) (Figure 2.6).

Lastly, the interaction between seed weight and animal body weight was also found to be reliable. It indicates that a one-unit increase in seed weight increases the odds of a positive to neutral interaction by 1.20 (SE = 1.04; 95% CI = 1.1-1.3) when there is a one-unit increase in animal body weight (Figure 2.6).

2.5 Discussion

Over 15 months and a total of 1439.2 hours of field observations, we documented 789 unique interactions involving the handling of fruits and/or seeds. These interactions unfolded between 19 distinct fruit-bearing plant species and a diverse array of 25 animal species, encompassing both individual species and various groups of animals.

Our observations revealed that large-seeded plants tended to have relatively fewer positive interactions compared to instances of neutral or negative interactions. Notably, a significant percentage of these interactions, whether positive, neutral, or negative, were facilitated by large frugivores, each weighing over 1 kilogram. The crucial role of large frugivores in dispersal networks, particularly for large-seeded plant taxa, has been extensively underscored in previous studies (Albert-Daviaud et al., 2022; McConkey et al., 2022; McConkey et al., 2018; Naniwadekar et al., 2019; Ong et al., 2021a; Qie et al., 2019; Vidal et al., 2013).

Our study contributes to this body of knowledge by highlighting the limited mutualistic interactions that certain large-seeded plants can experience when investigations simultaneously examine dispersers and predators.

Our network analysis highlighted the relatively poorer representation of species engaged in a higher proportion of positive interactions. In contrast, the generalist, large-bodied seed-predating bearded pig and the small-bodied Prevost's squirrel, which primarily engaged in neutral interactions, were the most connected and had the strongest associations with the plants they interacted with. Results from the linear mixed models also emphasized the lower odds of positive and neutral interactions (combined) with increasing animal body size. This trend can be explained by the high representation of seed-predating bearded pigs in this network. Bearded pigs have been recognized as important predators of dispersed seeds in Bornean forests (Curran and Leighton, 2000; Hautier et al., 2010). Our study highlights their role in frugivory networks as well.

The linear mixed models also indicated higher odds of positive and neutral interactions with increasing seed weight. This implies that factors beyond animal body size are at play. The heaviest seeds in our study belonged to *Canarium*, which were inaccessible to generalist seed predators like bearded pigs, requiring specialized seed predators such as tufted ground squirrels.

Interestingly, a broader range of smaller and larger animals, capable of either swallowing or carrying seeds, engaged in non-endozoochoric positive and neutral interactions with these seeds. This highlights the significance of seed dispersal abilities and underscores that body size alone is not the sole determinant, as emphasized by Ong et al., 2019b.

Among the nine frugivore species that participated in positive interactions, only a few, including Bornean white-bearded gibbons and muntjacs, engaged in higher proportions of positive interactions. In Asian forests, the crucial role of gibbons as significant frugivores, consuming fruit from a wide variety of plants and facilitating seed dispersal, has been extensively documented in multiple studies (Albert-Daviaud et al., 2022; Chen et al., 2023; Hai et al., 2018; McConkey et al., 2015; McConkey and Chivers, 2007; Ong et al., 2021a,b).

However, despite the potential constraints posed by large seed size on dispersal through endozoochory by gibbons (Chen et al., 2023), ungulates, such as sambar and muntjac, have shown effectiveness in dispersing large seeds through regurgitation (Brodie et al., 2009a,b; Prasad et al., 2006). They have been recognized as vital connector species in Southeast Asian frugivore networks (Albert-Daviaud et al., 2022). Their large body size and wide-ranging behavior, combined with their ability to handle hard fruits with large seeds, as observed in the case of muntjacs in our study, suggest that they may provide certain plants with non-redundant long-distance dispersal services. Nevertheless, their significance has often been underestimated (Sridhara et al., 2016).

We documented a single instance of sun bears engaging in endozoochory with *Willughbeia* sp. 1, a plant species in our study featuring the largest fruit with large seeds. While this plant attracted various animal species, the recorded endozoochory event was unique. Additionally, we observed seed spitting by larger primates and synzoochory by small squirrels in connection with this plant. However, the potential for long-distance dispersal was only evident in the case of sun bears, given their average home ranges of around 15 square km (Wong et al., 2004). While seed dispersal by bears in temperate regions has been extensively studied (García-Rodríguez et al., 2021), there is still a lack of knowledge regarding seed dispersal by tropical bear species (McConkey and Galetti, 1999; McConkey et al., 2018). Sun bears have been observed consuming fruits with large seeds and subsequently dispersing them through endozoochory, although they may not provide exclusive dispersal services (McConkey and Galetti, 1999).

In our analysis of the network, we documented the presence of at least five modules. Modularity within networks has been observed in hyper-diverse fruit-frugivore networks in other comparable SE Asian ecosystems (Albert-Daviaud et al., 2022; Ong et al., 2021a,b). The modularity we observed (0.296) was comparable to that reported for a network in Peninsular Malaysia, where modularity values of 0.297 and 0.294 were separately reported for frugivory and dispersal networks in previous studies (Ong et al., 2021a,b).

The organization into modules could be based on matching traits, such as fruit size and animal body size, as well as dietary specialization (Dalsgaard et al., 2017; Jordano, 2003; Mello et al., 2014), or even influenced by environmental variables (Encinas-Viso et al 2012).

Naniwadekar et al., (2019) in a south Asian forest and Albert-Daviaud et al., (2022) in a SE Asian forest noted that large-seeded trees and large-bodied avian frugivores like hornbills were organized into distinct modules. In neotropical forests, large-bodied terrestrial frugivores like tapirs were found to be important species in modules with plants bearing large fruit (Goebei et al., 2023).

In the modules we identified, no distinct patterns related to plant or animal traits or specialization emerged for four out of the five modules. This could be attributed to the presence of more generalist species, engaging in a larger number of neutral and negative interactions, in our network and perhaps the limited diversity in plant traits, considering the narrower range of plants studied compared to other studies (Albert-Daviaud et al., 2022; Naniwadekar et al., 2019; Ong et al., 2021b).

However, the fifth module stood out because it included fruiting plants with seeds encased in true stones (extremely tough protective coats) or large hard fruits (in the case of *Canarium* sp.), and a few animal species with the potential to handle them. This included the specialized seed predator, the tufted-ground squirrel, which had the morphological adaptations to access such seeds (Marshall et al., 2021), as well as the larger-bodied muntjacs, which were noted as the only species capable of swallowing whole large hard *Canarium* fruits.

Our network structure displayed a moderate level of specialization, suggesting that while some frugivores exhibit highly specific preferences for particular types of plants, many have more generalized interaction patterns. Additionally, the network exhibited low connectance, indicating that not all frugivores interacted with all available plants, resulting in sparse or less intense interactions between frugivores and plants.

Furthermore, our network demonstrated lower levels of nestedness, as indicated by a Weighted NODF value of 20.88, in contrast to disperser and predator networks observed in other Southeast Asian forests. Specifically, the disperser network exhibited Weighted NODF values ranging from 24.4 to 26.3, while the predator network ranged from 28.3 to 39.1 (Ong et al., 2021a,b). Moreover, a disperser network in a south Asian forest displayed a Weighted NODF value of 24.89 (Naniwadekar et al., 2019).

The observed low nestedness in our network suggests that large-fruited plants tend to attract distinct subsets of frugivorous species, leading to interactions that are not necessarily centered around more generalist mammals (Crestani et al., 2019; Goebei et al., 2023; Naniwadekar et al., 2019). This finding could be attributed to specialized plants, such as the *Canarium* species in our study, engaging in a higher number of interactions with specialized predators and large-bodied mutualists while having fewer interactions with other generalist species, in comparison to other plants studied that were accessible to a broader range of animal visitors.

In summary, this study uncovers a modular yet less nested (compared to networks in other SE Asia forests) frugivore-plant interaction network, characterized by a moderate level of specialization. Notably, large animals played a disproportionately significant role in mediating interactions. Large-seeded plants in our study primarily experienced more antagonistic interactions than mutualistic ones, with large-bodied animals being responsible for the majority of both mutualistic and antagonistic interactions. Importantly, some of the key large-bodied mutualists and antagonists in this network are currently classified as Endangered, Vulnerable, and Near Threatened (IUCN, 2022).

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2.8 Tables and figures

Table 2.1. Common and scientific names of animal species and groups that interacted with the studied large-seeded plants, including their body weights and current IUCN Status/Population trend data retrieved from https://www.iucnredlist.org/ in September 2023

Common name	**Scientific name**	**IUCN status**	**IUCN population trend**	**Weight (kg)**
Banded civet	*Hemigalus derbyanus*	NT	Decreasing	4.4
Bearded pig	*Sus barbatus*	VU	Decreasing	130
Binturong	*Arctictis binturong*	VU	Decreasing	8
Bornean crested fireback	*Lophura ignita*	VU	Decreasing	1.9
Bornean orangutan	*Pongo pygmaeus*	CR	Decreasing	67.5
Bornean white-bearded gibbon	*Hylobates albibarbis*	EN	Decreasing	6
Emerald dove	*Chalcophaps indica*	LC	Decreasing	0.1
Long-tailed macaque	*Macaca fascicularis*	EN	Decreasing	5
Long-tailed porcupine	*Trichys fasciculata*	LC	Decreasing	1.8
Malay civet	*Viverra tangalunga*	LC	Stable	3.9
Malayan porcupine	*Hystrix brachyura*	LC	Decreasing	8
Mouse deer	*Tragulus napu*	LC	Decreasing	4.3
	Tragulus kanchil	LC	Decreasing	2.3
Muntjac	*Muntiacus muntjak*	LC	Decreasing	24
	Muntiacus atherodes	NT	Decreasing	18
Pale giant squirrel	*Ratufa affinis*	NT	Decreasing	1.2
Palm civet	*Arctogalidia trivirgata*	LC	Decreasing	3.3
	Paradoxurus hermaphroditus	LC	decreasing	2.5
Prevost's Squirrel	*Callosciurus prevostii*	LC	Decreasing	0.4
Rat species	*na*	na	na	<1
Red langur	*Presbytis rubicunda*	Vu	Decreasing	6.3
Small squirrel species	*Callosciurus sp.*	LC	na	<0.3
Southern pig-tailed macaque	*Macaca nemestrina*	EN	Decreasing	6.5
Three-striped ground squirrel	*Lariscus insignis*	LC	Decreasing	0.2
Sun bear	*Helarctos malayanus*	VU	Decreasing	42.5
Thick-spined porcupine	*Hystrix crassispinis*	LC	Stable	4.6
Tufted ground squirrel	*Rheithrosciurus macrotis*	VU	Decreasing	1.3
Yellow-throated marten	*Martes flavigula*	LC	Decreasing	4.1

Table 2.2. Number and proportions (with respect to the total number of interactions for each species) of positive, neutral, and negative interactions. interactions were classified as follows: positive—swallowing whole fruit or pulp and seeds and carrying away whole or partially eaten fruits; neutral—consuming pulp while dropping or spitting out intact seeds under the parent plant, dropping whole or partially eaten fruit under the parent plant, and feeding on fruit while still attached to the parent plant (in situ); and negative—carrying away intact seeds, and/or feeding on seeds.

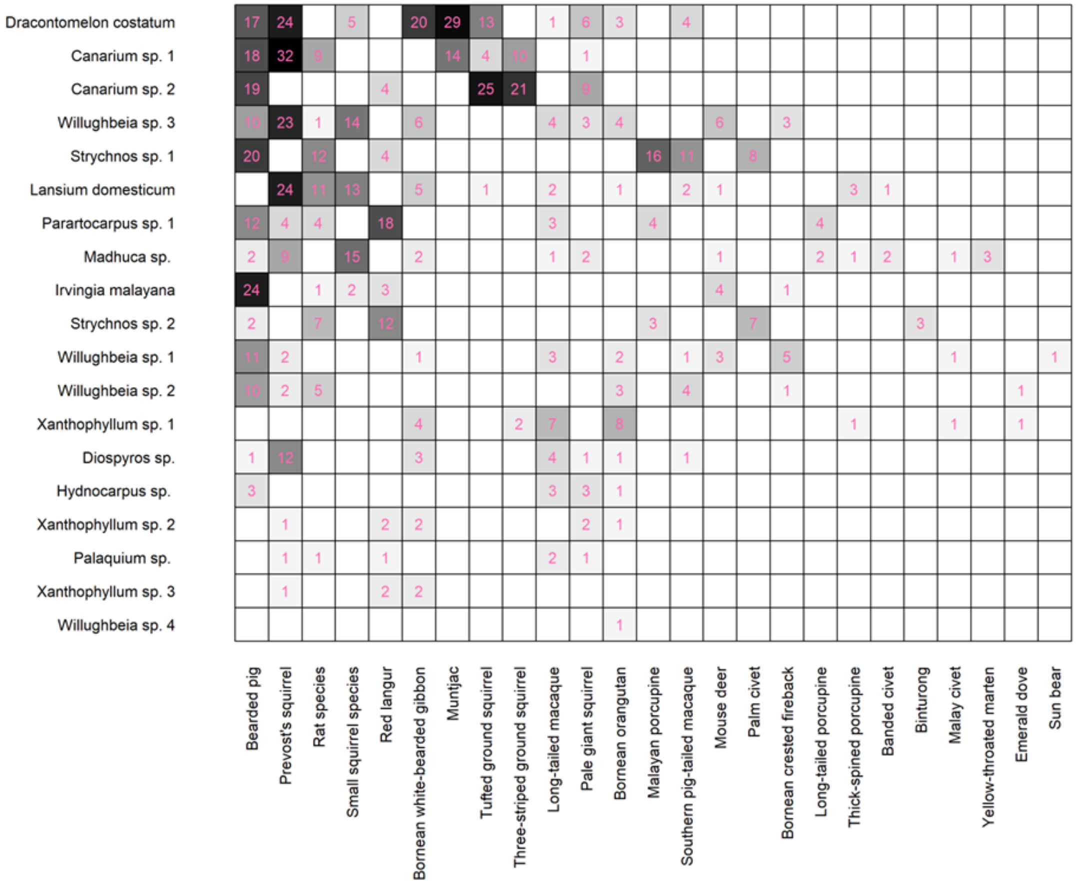
fruit- and seed-eating animals	**positive**	**neutral**	**negative**	**%positive**	**%neutral**	**%negative**
Banded civet	0	0	3	0.00	0.00	1.00
Bearded pig	0	20	126	0.00	0.14	0.86
Binturong	3	6	0	0.33	0.67	0.00
Bornean crested fireback	0	1	9	0.00	0.10	0.90
Bornean orangutan	14	21	2	0.38	0.57	0.05
Bornean white-bearded gibbon	39	37	0	0.51	0.49	0.00
Emerald dove	0	0	2	0.00	0.00	1.00
Long-tailed macaque	3	47	26	0.04	0.62	0.34
Long-tailed porcupine	0	0	6	0.00	0.00	1.00
Malay civet	0	0	3	0.00	0.00	1.00
Malayan porcupine	0	0	23	0.00	0.00	1.00
Mouse deer	0	0	15	0.00	0.00	1.00
Muntjac	29	24	0	0.55	0.45	0.00
Pale giant squirrel	1	39	3	0.02	0.91	0.07
Palm civet	14	26	0	0.35	0.65	0.00
Prevost's squirrel	40	216	13	0.15	0.80	0.05
Rat species	0	0	51	0.00	0.00	1.00
Red langur	0	53	39	0.00	0.58	0.42
Small squirrel species	5	56	4	0.08	0.86	0.06
Southern pig-tailed macaque	1	2	22	0.04	0.08	0.88
Three-striped ground squirrel	1	0	32	0.03	0.00	0.97
Sun bear	1	0	0	1.00	0.00	0.00
Thick-spined porcupine	0	0	5	0.00	0.00	1.00
Tufted ground squirrel	0	11	41	0.00	0.21	0.79
Yellow-throated marten	0	7	0	0.00	1.00	0.00

Table 2.3. Degree and strength, which are species-level network indices, for individual animal species or groups within the bipartite network of large-seeded plant species. Species degree indicates the number of plant species the seed predator interacts with, reflecting the diversity of partners each predator engages with. Species strength summarizes the dependencies between species, capturing the level of interdependence within the network. Interaction strength (b_{ij}) represents the proportion of species i's interactions with a specific partner (species j) relative to the total registered interactions for species i.

animal visitors	**degree**	**species strength**
Bearded pig	13	3.14
Prevost's squirrel	12	2.7
Bornean orangutan	10	1.88
Long-tailed macaque	10	1.38
Bornean white-bearded gibbon	9	1.35
Pale giant squirrel	9	1.02
Rat species	9	1.13
Red langur	8	1.73
Southern pig-tailed macaque	6	0.45
Mouse deer	5	0.34
Small squirrel species	5	0.86
Bornean crested fireback	4	0.27
Tufted ground squirrel	4	0.49
Malay civet	3	0.1
Malayan porcupine	3	0.4
Three-striped ground squirrel	3	0.5
Thick-spined porcupine	3	0.11
Banded civet	2	0.06
Emerald dove	2	0.08
Long-tailed porcupine	2	0.13
Muntjac	2	0.4
Palm civet	2	0.32
Binturong	1	0.09
Sun bear	1	0.03
Yellow-throated marten	1	0.07

Table 2.4. Degree and strength, which are species-level network indices, for each plant species within the bipartite network. Species degree indicates the number of plant species with which the seed predator interacts, reflecting the diversity of partners each predator engages with. Species strength, on the other hand, represents the sum of dependencies between species, capturing the level of interdependence within the network. Interaction strength (b_{ij}) signifies the proportion of species i's interactions with a specific partner (species j) relative to the total registered interactions for species i.

plant species	**degree**	**species strength**
Madhuca sp.	12	3.14
Lansium domesticum	11	1.99
Dracontomelon costatum	10	2.36
Willughbeia sp. 1	10	2.37
Willughbeia sp. 3	10	1.78
Canarium sp. 1	7	1.29
Diospyros sp.	7	0.41
Parartocarpus sp.	7	1.52
Willughbeia sp. 2	7	1.07
Xanthophyllum sp. 1	7	1.74
Irvingia malayana	6	0.65
Strychnos sp. 1	6	2.16
Strychnos sp. 2	6	2.01
Canarium sp. 2	5	1.75
Palaquium sp.	5	0.15
Xanthophyllum sp. 2	5	0.21
Hydnocarpus sp.	4	0.27
Xanthophyllum sp. 3	3	0.1
Willughbeia sp. 4	1	0.04



	Bearded pig	Prevost's squirrel	Rat species	Small squirrel species	Red langur	Bornean white-bearded gibbon	Muntjac	Tufted ground squirrel	Three-striped ground squirrel	Long-tailed macaque	Pale giant squirrel	Bornean orangutan	Malayan porcupine	Southern pig-tailed macaque	Mouse deer	Palm civet	Bornean crested fireback	Long-tailed porcupine	Thick-spined porcupine	Banded civet	Binturong	Malay civet	Yellow-throated marten	Emerald dove	Sun bear
Dracontomelon costatum	17	24		5		20	29	13		1	6	3		4											
Canarium sp. 1	18	32	9				14	4	10		1														
Canarium sp. 2	19				4			25	21		9														
Willughbeia sp. 3	10	23	1	14		6				4	3	4			6		3								
Strychnos sp. 1	20		12		4								16	11		8									
Lansium domesticum		24	11	13		5		1		2		1		2	1				3	1					
Parartocarpus sp. 1	12	4	4		18					3			4					4							
Madhuca sp.	2	9		15		2				1	2				1			2	1	2		1	3		
Irvingia malayana	24		1	2	3										4		1								
Strychnos sp. 2	2		7		12								3			7					3				
Willughbeia sp. 1	11	2				1				3		2		1	3		5					1			1
Willughbeia sp. 2	10	2	5									3		4			1							1	
Xanthophyllum sp. 1						4			2	7		8							1			1		1	
Diospyros sp.	1	12				3				4	1	1		1											
Hydnocarpus sp.	3									3	3	1													
Xanthophyllum sp. 2		1			2	2					2	1													
Palaquium sp.		1	1		1					2	1														
Xanthophyllum sp. 3		1			2	2																			
Willughbeia sp. 4												1													

Figure 2.1. Bipartite network illustrating interaction events recorded between each animal species/group (x-axis) and each plant species (y-axis) in our study. Shaded squares indicate realized interactions, and white squares indicate no interaction between the corresponding plant and animal species. The darker squares indicate a higher number of interactions, and the values in pink indicate the number of interactions.

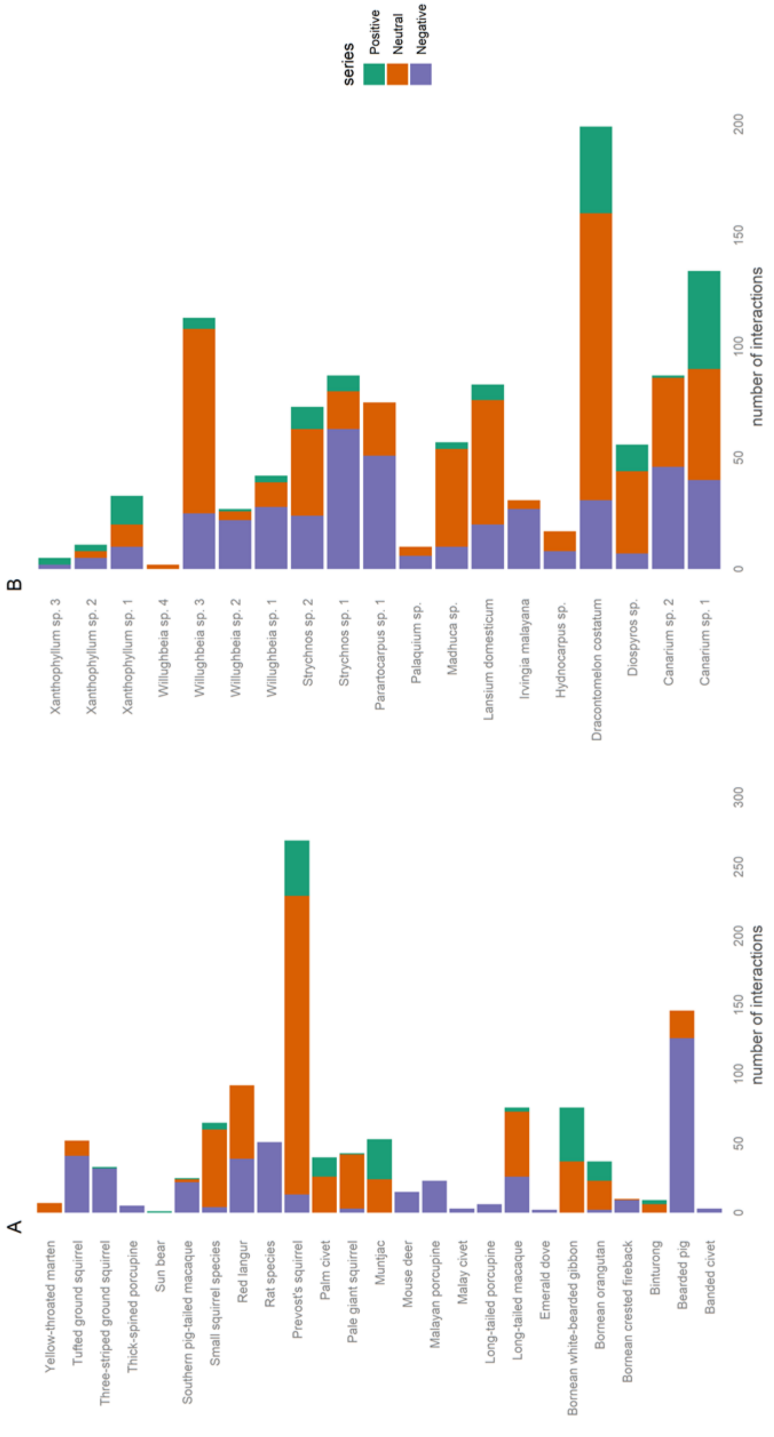


Figure 2.2. Counts of interaction events (positive, neutral, and negative) across animal and plant species. Positive interactions include swallowing (including both pulp and seeds) and carrying away whole or partially eaten fruits, while neutral interactions involve consuming pulp while dropping or spitting out intact seeds, dropping whole fruits, and feeding on fruit while still attached to the parent plant (in situ). Negative interactions consist of carrying away intact seeds, with or without pulp, and/or feeding on seeds.

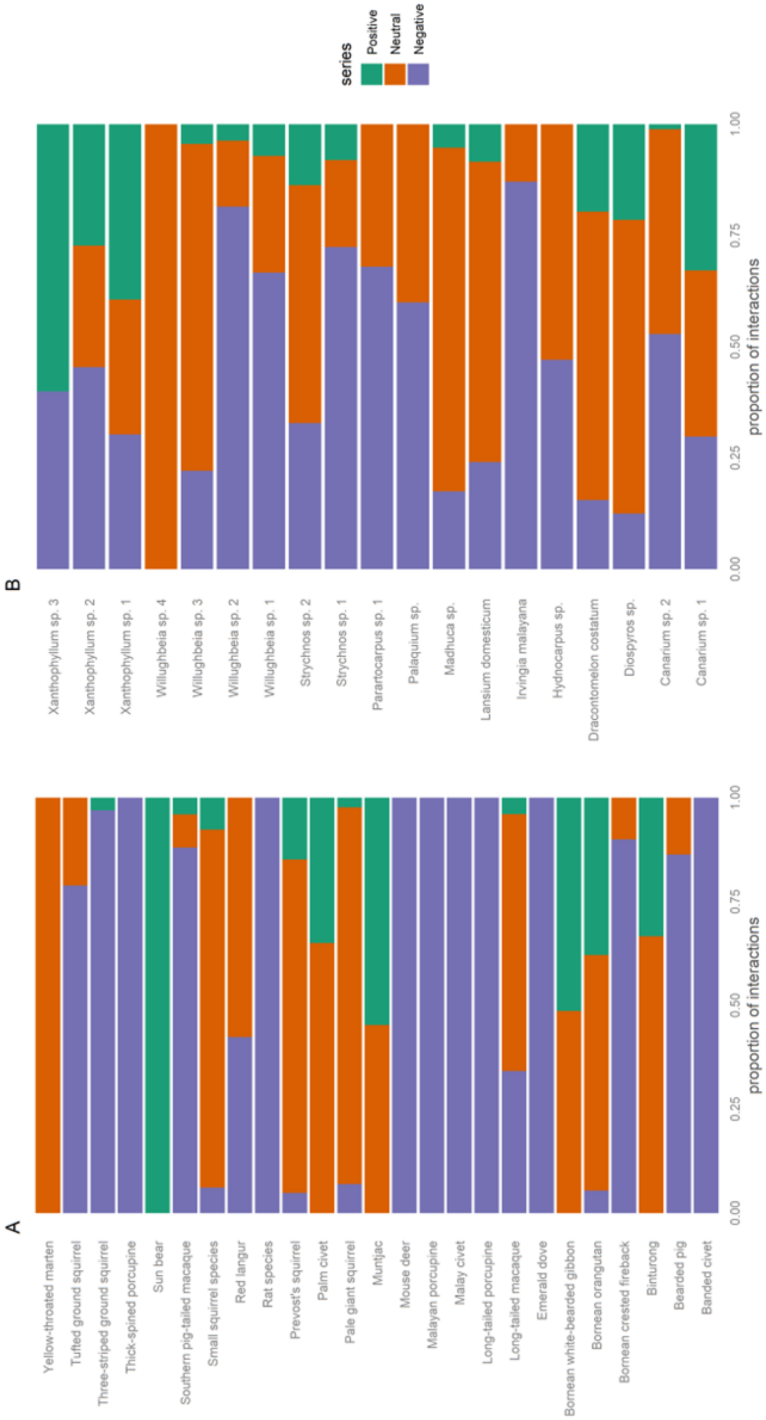


Figure 2.3. Proportion of interaction events (positive, neutral, and negative) across animal and plant species. Positive interactions include swallowing (including both pulp and seeds) and carrying away whole or partially eaten fruits, while neutral interactions involve consuming pulp while dropping or spitting out intact seeds, dropping whole fruits, and feeding on fruit while still attached to the parent plant (in situ). Negative interactions consist of carrying away intact seeds, with or without pulp, and/or feeding on seeds.

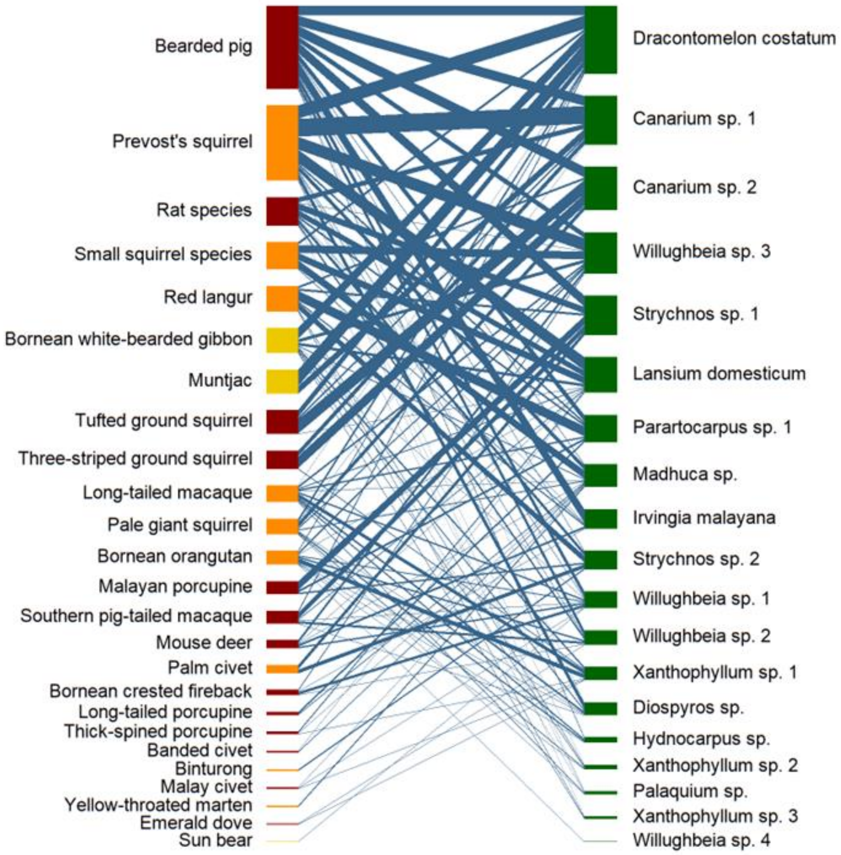


Figure 2.4. Bipartite network illustrating interaction events recorded between each animal species/group and each plant species in our study. The left axis, represented by maroon, orange, and yellow nodes, indicates animal visitors and their interaction types: maroon represents predominantly predatory species (proportion of negative interactions >0.5), orange represents predominantly neutral animal interactions, and yellow features key mutualists (proportion of positive interactions >0.5). The green bars on the right represent various large-seeded plant species. Blue links signify the number of connections, with the width of the links representing the number of interactions between the corresponding animal and plant species. Node width, represented by the height of rectangles, reflects species representation; on the animal axis, it indicates the total number of interactions by that species, while on the plant axis, it denotes the total number of interactions received by the plant species. This visualization provides a comprehensive overview of ecological interactions in our study.

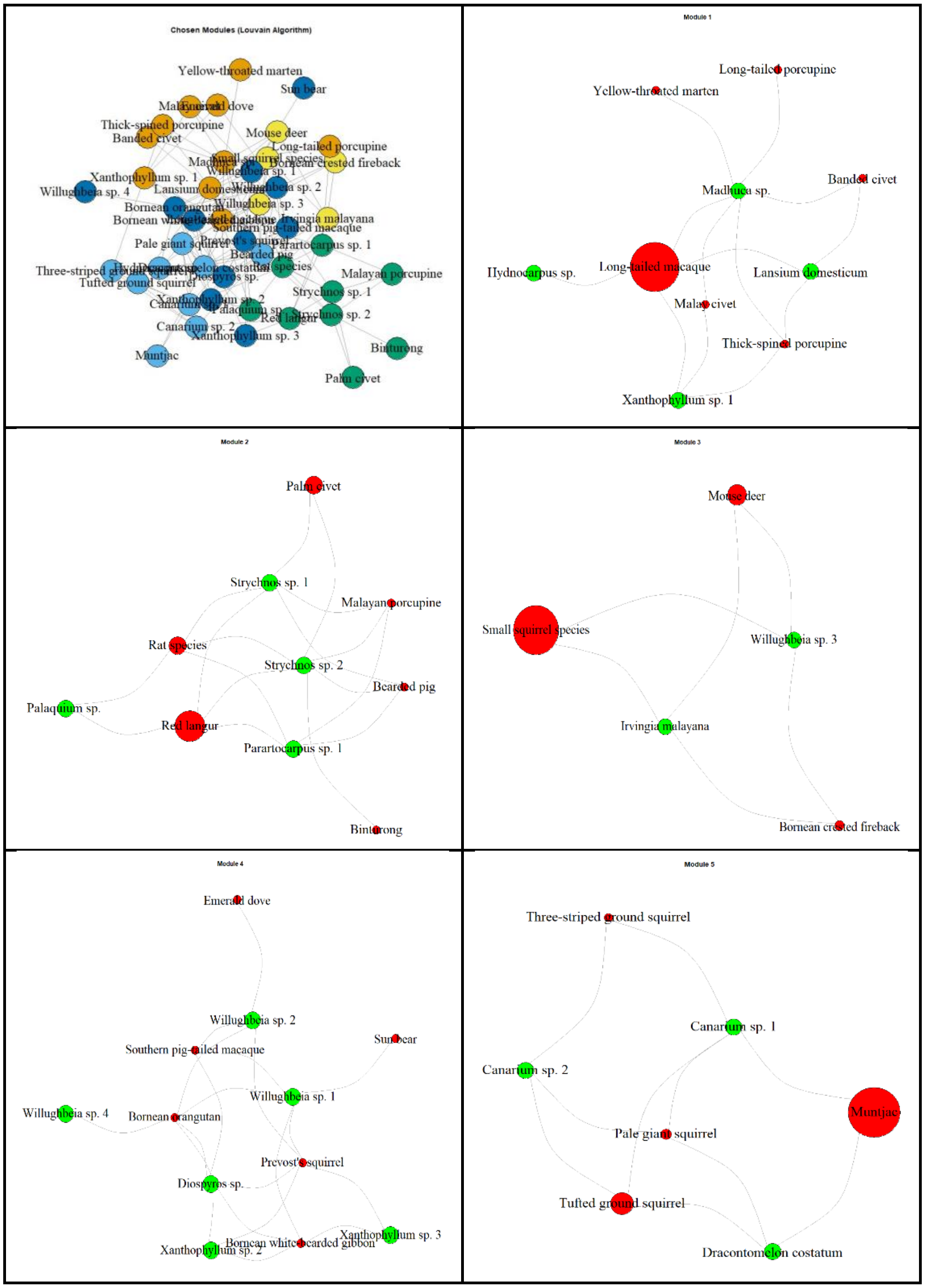


Figure 2.5. Highest modularity composition obtained by running the Louvain algorithm 50 times, designed for detecting clusters in bipartite networks. This composition unveils five modules in the interaction network of fruit/seed-eating animals and large-seeded plant species, as shown in the top-left panel. Circles depict nodes (species), and lines represent links between animal and plant species. Colored nodes denote distinct modules or clusters of tightly connected species. The remaining panels show each of the five modules separately, with animal node size (represented by red circles) weighted based on the total number of interactions. The size of plant nodes (represented by green circles) is held constant.

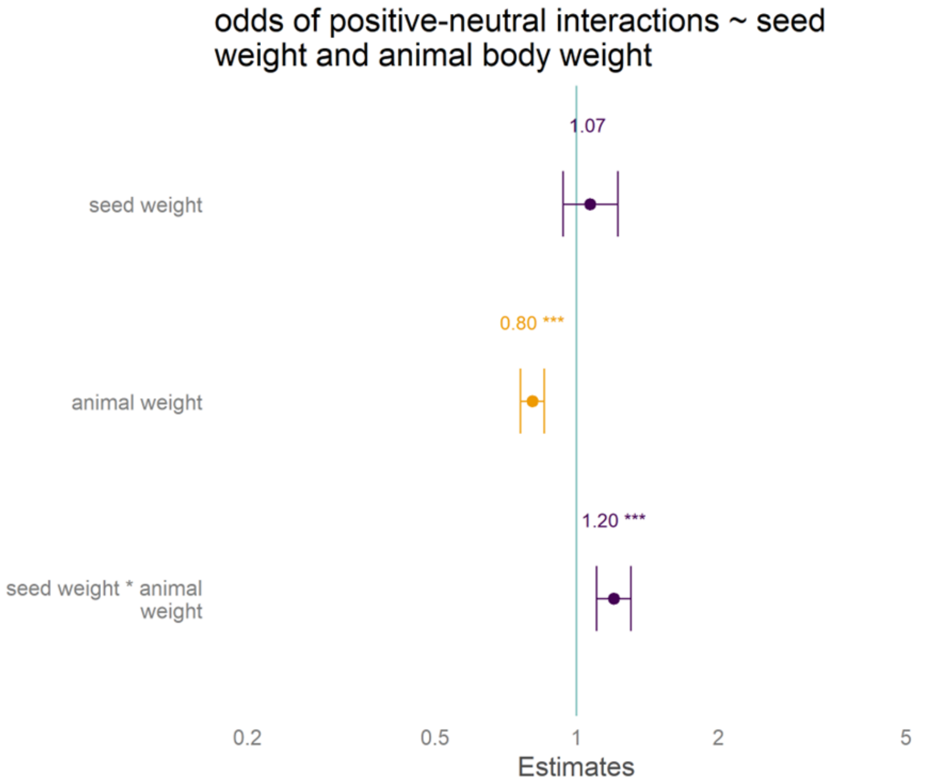


Figure 2.6. Odds of positive and neutral interactions (combined) in relation to the interaction between seed weight and animal body weight. The coefficient plot provides estimates derived from the best model, depicting the size and direction of the effects of seed weight, animal weight, and their interaction. Coefficients and confidence interval boundaries, originally in the log-odds scale, have been transformed to their original scale. The exact exponentiated values are presented above each bar. Points on the graph represent coefficient estimates, while error bars represent 95% confidence intervals.

Chapter 3: To Eat or to Move: Investigating Mutualistic and Non-Mutualistic Interactions Within a Seed Predator Network in a Lowland Rainforest in Indonesian Borneo

3.1 Abstract

Interactions between plants and animals, as well as biotic agents such as fungi, are pivotal in shaping diversity within plant communities. Seed predation constitutes one such interaction, wherein a diverse array of seed predators modify primary seed shadows in distinct ways, influenced by factors such as resource availability, seed traits, and their own biology. The outcomes of these interactions have varying effects on seed mortality and establishment. Therefore, evaluating multispecies interactions becomes imperative to understand their collective influence on plant reproductive success. During a 13-month study, we examined the post-dispersal fate of 20 large-seeded lowland tropical rainforest plants encompassing 15 species. Our goals were to a) document seed predator assemblages, b) assess seed handling behavior, and c) identify how different predators respond to seed density, proximity to parent plant, and traits, and subsequently influence seed fate. We tracked 963 tagged seeds positioned at different densities and distances from parent plants, observing their fate via camera traps and periodic visits until seed death, establishment, or loss. Our results revealed a diverse guild of predators including ungulates, a primate, a bird, rodents, invertebrates, and fungi interacting with seeds. Seeds placed farther from parents experienced lower predation rates, while seeds in high-density clusters under the canopy fared better than medium- and low-density clusters. Vertebrate seed predators,

particularly large- and small-bodied generalists, contributed the most to seed mortality. Seed size and seed coat robustness influenced seed handling behavior (predation and caching) differently among predatory species.

3.2 Introduction

Mutualistic and antagonistic interactions between plants and animals, as well as other biotic agents such as fungi, are considered critical to the structuring of plant communities and shaping species diversity (Bagchi et al., 2014; Germain et al., 2013; Jia et al., 2018; Wang and Smith, 2002). In tropical forests, many woody plants produce fleshy fruits to attract frugivorous animals, which in turn disperse their seeds (Corlett, 2017).

Primary dispersers, comprising both arboreal and terrestrial fruit-eating animals, aid in the seed dispersal process through defecation following whole fruit ingestion (McConkey and Chivers, 2009), regurgitation (Delibes et al., 2019; Kitamura, 2011), spitting and/or dropping (Butler and Johnson, 2022; Dominy and Duncan, 2005; Tsuji and Su, 2018). Consequently, seeds are distributed at various distances and densities from their parent plants, contingent on the distinct behaviors of the dispersing animal species (Borah and Beckman, 2021; McConkey et al., 2014; Morales et al., 2013; Rehm et al., 2019; Russo et al., 2006).

These initial templates of seed deposition, or seed shadows, are further modified by post-dispersal seed predation and secondary dispersal by specialist and generalist seed predators, including but not limited to fungi, invertebrates, birds, rodents, and ungulates (Hautier et al., 2010; Lecompte et al., 2017; Loayza et al., 2020; Perea et al., 2014; Williams et al., 2021; Yu et al., 2022). Several factors influence how the seed shadows of primary dispersal agents are modified by predators (Lichti et al., 2017).

Studies on post-dispersal seed fate have observed conspecific negative density or distance dependent patterns of seed mortality in support of the Janzen-Connell hypothesis. Janzen (1970) and Connell (1971) posited that specialized host-specific insect and fungal enemies kill an increasingly greater proportion of seeds at distances proximate to parent plants (distance dependence). They excessively target patches with higher seed densities, typically found below or near parent plants (conspecific negative density dependence); therefore, seed mortality is expected to be most pronounced around the parent plant. Thus, seed predation serves to minimize the accumulation of conspecifics at natal sites, consequently promoting the recruitment of heterospecific species, and promoting diversity (Bagchi et al., 2014; Levi et al., 2018; Terborgh, 2012).

Through a comprehensive meta-analysis of studies that tested predictions of the Janzen-Connell hypothesis, Comita et al., (2014) found corroborating evidence of reduced survival rates, particularly during the seedling stage (which was the focus of most studies), in close proximity to conspecifics and in regions with high conspecific densities. However, wide variations have been reported in the magnitude of conspecific negative density or distance-dependent effects across studies, as well as limited evidence supporting the idea that specialized enemies drive these patterns, as suggested by the Janzen-Connell hypothesis. The observed variability is not surprising, given the differences across environments, in plant and animal traits, and in predator assemblages.

Abiotic conditions, such as higher moisture levels in tropical forests (Comita et al., 2014), snowfall in temperate areas (Lorens et al., 2011), or seasonality (Rusch et al., 2014) influence predator prevalence and behavior, seed mortality, and survival patterns. Biotic factors, like resource abundance (Bagchi et al., 2011; Curran and Leighton, 2000; Jansen et al., 2004;

Kelly and Stork, 2002; Liu et al., 2013), along with environmental heterogeneity (Dally et al., 2004; Li et al., 2023) can lead to differences in seed predation and hoarding behavior.

Seed traits, such as size, mechanical and chemical defenses, and nutrient content, affect seed predation and removal. The impact of seed size on predation by small mammals is highly variable, with different studies showing preferences for large (Chang et al., 2009; Mittleman et al., 2021; Paine et al., 2016; Wang and Chen, 2009), medium (Gopal et al., 2021; Rusch et al., 2013), or small-sized seeds (Sidhu and Datta, 2015). Larger seeds are often hoarded further away, while smaller seeds face higher onsite predation (Kuperwicz and García-Robledo, 2019; Lai et al., 2014; Luo et al., 2023; Xiao et al., 2005), although survival rates have been shown to vary for small, medium, and large seeds over time (Cao et al., 2016) and space (Lai et al., 2014).

Mechanically well-defended seeds are more likely to be removed than immediately consumed (Lai et al., 2014; Sidhu and Datta, 2012; Vander Wall, 2010), possibly because they are better protected against fungal attack (Dalling et al., 2011), have longer periods of dormancy (Steele et al., 2001; Sundaram et al., 2018), and/or involve extended handling time (Chang and Zhang, 2014; Jacobs, 1992). Rodents show a preference for seeds with high nutrient content, leading to increased predation and reduced dispersal of nutrient-rich seeds compared to nutrient-poor, high-fiber seeds (Yadok et al., 2020). While chemically defended seeds may be less appealing to rodents (Chang et al., 2009; Jansen et al., 2004; Vander Wall, 2010), the presence of valuable nutrients may lead them to scatter-hoard larger chemically defended seeds with higher nutritional value over undefended smaller seeds with lower nutritional value, which are immediately consumed (Wang and Yang, 2015).

Traits such as body size, nutritional requirements, and morphological and physiological adaptations of hoarding and non-hoarding seed predators can significantly influence the patterns of seed predation and secondary dispersal. Larger hoarders are adept at harvesting, consuming, and transporting larger seeds over longer distances (Kuprewicz and García-Robledo, 2019; Mittelman et al., 2021; Rosin and Poulsen, 2017). Smaller rodents, possibly constrained by their body size, disproportionately prey on, and remove smaller seeds (Sidhu and Datta, 2015). Hoarding species further benefit from spatial memory and a keen sense of smell for effective seed storage, monitoring, retrieval, and pilfering of cached seeds (Vander Wall and Jenkins, 2003; Yi et al., 2021).

Non-hoarding species, such as bearded pigs that forage across larger areas, reduce the survival of heterospecific seeds, particularly larger seeds, in both areas of low and high seed densities (Hautier et al., 2010), negating the advantage that plants would gain from distance-dependent processes. Finally, morphological adaptations, as seen in specialist seed predators like tufted ground squirrels that allow them to feed on seeds with extremely hard coats (Marshall et al., 2021), and physiological adaptations seen in some rodent species that allow them to detoxify acutely toxic seeds (Sherbrooke, 1976; Yoshikawa et al., 2018), enable them to disproportionately harvest seeds of certain plant species.

Although interactions between seed predators and seeds are often characterized as antagonistic, mounting evidence suggests that certain seed predators can also act as dispersers, occupying a more intermediate position along the antagonistic-mutualistic continuum (Leeuwen, 2022). In tropical terrestrial ecosystems, rodents play a prominent role in providing effective secondary dispersal services to plants (Briggs et al., 2009; Godo et al., 2021; Jansen et al., 2012). They exhibit scatter-hoarding behavior, transporting seeds away from conspecific plants and hiding them at several scattered caching locations (Brodin 2010; Hirsch et al., 2012).

Seeds are typically buried under soil or leafy debris for later consumption during periods of resource scarcity (Jansen et al., 2002). This behavior results in a low-density distribution of seeds, creating optimal conditions for seed survival against predation and promoting germination (Geluso, 2022). Both low densities and burial contribute to reduced detectability (Geluso, 2022), while the burial itself may create favorable conditions for germination (Dracxler and Forget, 2017) but could also negatively impact seedling survival (Zhang et al., 2022).

Cache owners are known to actively monitor their caches to protect seeds from theft (Brodin, 2010; Hirsch et al., 2013) and periodically re-cache seeds, especially larger ones (Jansen et al., 2012; Wang et al., 2014), at locations further away (Jansen et al., 2012). This behavior enhances long-distance dispersal and improves survival (Jansen et al., 2012; Wang et al., 2019). Consequently, since not all seeds are recaptured by cache owners from isolated caches, the likelihood of successful germination, establishment, and subsequent recruitment of plants is increased (Jansen et al., 2012; Steele et al., 2011). However, the proportion of seeds that escape predation in this manner has been found to be highly variable (Vander Wall and Jenkins, 2003).

Our current understanding of post-dispersal seed fate processes is largely based on extensive research in neotropical and temperate regions with vastly different seed predator assemblages. However, a substantial knowledge gap on the intricacies of post-dispersal seed fate persists regarding Southeast Asian forests, known for exceptional plant diversity (Bruyn et al., 2014; Corlett 2007). At our site, the seed predator assemblage is diverse, encompassing large-bodied (>1 kg) pigs, porcupines, and squirrels, small-bodied (<1 kg) squirrels and rats, as well as invertebrates and fungi. The variations in body size, mobility, behavior within a diverse seed predator network such as this can lead to significant variability in their impact on seed mortality (Lichti et al., 2017).

To grasp the cumulative impacts of seed predator assemblages on the reproductive success of plants, it is essential to study multispecies interactions. In this study, we experimentally assessed the post-dispersal seed fate for several large-seeded (>15 mm in length in this study) lowland tropical rainforest plants. Our objectives were to: a) document seed predator assemblages in our study area, b) construct a seed predator network to understand the relative importance of different predatory species in influencing the seed fate of the plants under study, c) assess seed handling behavior, and d) quantify how seed density, proximity to parent plants, and seed traits influence seed fate.

3.3 Methods

3.3.1 Field methods

We collected data over 12 months: from November 2019 to May 2020, and from August to December 2020. Our study was conducted during the intermast period. Most forest types in our ecosystem are characterized by frequent and prolonged periods of low fruit production between mast fruiting events (Marshall et al., 2009) and no discernible annual pattern in fruit phenology (Cannon et al., 2007). We therefore could not preselect large-seeded plant species for our study. Instead, we included individuals and species that fruited during the study period. To locate plants bearing fruit, we walked along existing trails and searched select locations off trails, thoroughly scanning the canopy and the forest floor for fruits and seeds. We also relied on sounds of animal activity to locate fruiting plants, especially those with large fruits (specifically *Canarium* sp. and *Willughbeia* sp.) that were clearly audible when they fell to the forest floor.

Finally, we frequently checked in with other researchers working at the research site for information on the location of fruiting plants (e.g., inside long-term phenology plots).

Focal plant individuals were separated from each other in space and/or time (Figure 3.1); each monitored plant stem was at least 100m from any other monitored stem that was producing fruit concurrently, with one exception when one individual of *Diospyros* sp., *Willughbeia* sp. 1, and *Palaquium* sp. each were fruiting at the same time within 100m of one another. We assessed the fate of seeds from 20 individuals belonging to 15 plant species and 10 families, that included trees and lianas (Table 3.1; Box B3.1). Seeds collected to assess seed fate included intact seeds extracted from ripe fruit and intact seeds collected from the forest floor. All seeds were thoroughly examined so that seeds with insect activity and/or fungal presence were excluded from our sample.

Selected seeds were brought back to our lab at the research station, where we cleaned them without damaging the seed coat and measured their length, width, thickness and weight, using a Mitutoyo high-precision digital caliper and a Fristaden Lab Digital Precision Analytical Balance Lab Scale (1000g x 0.01g scale, 0.01g accuracy). We described seed protection for each species as follows: 'soft' (capable of being broken by fingernail), 'hard' (resistant to breakage by fingernail), and 'stone' (seeds with true stones). Each seed was then tagged with brightly colored braided fishing line (50-100cm long) affixed using Loctite Super Glue (Sidhu and Datta, 2015). The free end of the fishing line was attached to a tag bearing a unique number. Thereafter, the seeds were returned to the ground below their parent plants for seed fate assessment. We returned the seeds to the location within a day or two after collection, except in the cases of *Canarium* and *Dracontomelon* seeds, where cleaning (removing fruit pulp from the seed) took more time, and together with measuring and tagging, was completed over three days.

We expected seeds to be deposited in different densities and at varying distances by animals dispersing seeds (Nathan and Muller-Landau, 2000; Rehm et al., 2019; Russo et al., 2007). Additionally, we expected high rodent activity at the parent plant, but also expected rodents to search the forest floor for seeds at sites away from the parent plant (Rosin and Poulsen, 2017). Taking this into account, we stationed seeds within a 2x2m area in different densities (low-1, medium-5, high-10) and at varying distances from the crown of the parent plant (0m, 25m, and 50m), along three randomly selected directions radiating away from the plant. We monitored 48 seeds per individual plant, except for one individual *Diospyros* tree where we also monitored three extra seeds placed at three additional stations (representing low density stations at varying distances from the parent plant). This was a special case where we compared seed fate of lab cleaned seeds and seeds spat out by animals with some fruit pulp still attached (Box B3.2). In total, we monitored the fate of 963 seeds across 183 seed stations.

At each seed station we cleared (some) leaf litter, without significantly altering the substrate, before laying down tagged seeds. We positioned a camera trap (Bushnell 16MP Trophy Cam HD Essential E3 Trail Camera) at every station (except 3 stations) such that it would record 20 second videos when triggered by animals that visited or passed through the seed station. These videos were used to identify seed eating and caching species and to observe seed handling behavior (predation, partial predation, and removal from seed station). Cameras remained at the station until the last seed was removed, or until seeds present at the seed station transitioned into the seedling stage, whichever occurred earlier. Based on availability of cameras, some caching sites were monitored with camera traps until seed death or removal. We visited seed stations once every 3 days until all seeds were lost (by removal or death) or had emerged as seedlings. Seedlings were tagged and monitored once every three months until they died or until the end of the study.

During each visit to the seed station, we examined all seeds thoroughly and kept detailed notes on the status of each seed. Specifically, we noted if seeds (a) were intact, (b) were fully or partially preyed upon by vertebrates and/or invertebrates, (c) had germinated, (d) were removed, and/or (e) had fungus. We searched the area around the seed station up to 20 m thoroughly to locate seeds that were moved away and preyed upon or cached. The brightly colored seed tags helped locate such seeds. When caching sites were located, data on cache type (larder vs. scatter hoarding), substrate, distance from seed station, and status of the seed were noted. When we were unable to locate seeds that were moved away from the seed station, they were noted as ‘lost’. Before leaving each station, we cleared the seed station (2x2m area) to keep it free from other fallen fruit and seeds.

3.3.2 Analytical methods

We used the R statistical and programming environment for data analysis and visualization (R Core Team, 2021).

We calculated and plotted the total number of seeds recorded within each seed fate category. Some seeds were counted under multiple categories. For example, a seed that was first cached, germinated later, but was eventually preyed upon, would feature under the three respective categories. We utilized camera trap data and field observations to compute the number of seeds preyed upon or removed by various animal species. Notably, all rat species were grouped under a single category: 'rats,' as we could not reliably identify them at the genus and species level.

We further calculated the proportion of seeds consumed by seed predators at different densities, distances from the parent plant, and seed protection categories. We calculated the quantity of germinated seeds consumed or removed by different seed predators. Additionally, we analyzed the time it took for different plant species to germinate, taking into account the associated seed protection categories.

Our analysis further included calculating the number of cached seeds, tracking the distances to which seeds were relocated, identifying the types of caching locations based on animal species, and documenting the plant species whose seeds were subject to caching. We quantified the number of seeds that were re-cached, both by plant species and hoarding species. We also assessed the duration for which seeds remained in primary, secondary, tertiary, and quaternary caches, either until they died or until the end of our study.

Lastly, we computed the proportions of intact seeds, viable seeds showing signs of insect activity and/or fungal growth, germinated seeds, and surviving seedlings at the end of our study. We also determined the proportions of survivors at natal sites versus cache sites.

We visualized interactions between seed predators and individual plant species through a bipartite network diagram using the {bipartite} package's plotweb() function (Dormann et al., 2008). The construction of the network diagram was based on the total number of seed predation and removal (representing lost seeds) events by vertebrates, invertebrates, and fungi for each animal species or broader taxa across all individuals of each plant species. Given our limitations in identifying most insect species and all fungi, we aggregated these interactions into two general categories: 'invertebrates' and 'fungi.' These categories were then included in the network. Lastly, we calculated two network indices—degree and strength—for each species or group of seed predators within the network. Species degree indicates the number of plant species the seed predator interacts with, reflecting the diversity of partners each predator engages with. Species strength, on the other hand, captures the level of interdependence within the network. Interaction strength (b_{ij}) signifies the proportion of species *i*'s interactions with a specific partner (species *j*) in relation to the total registered interactions for species *i* (Bascompte et al., 2006). For this we used the specieslevel() function from the {bipartite} package (Dormann et al., 2008; Dormann, 2011).

Next, we fitted a Cox Proportional Hazards Model, a semi-parametric time-to-event survival analysis, to our seed removal data. We used this method to examine how the covariates —distance and density— influenced the risk that an event (total seed loss, or presence of viable seeds) occurred at a particular point in time. The measure of risk is expressed as a hazard ratio, where a value of 1 indicates that the risk of the event occurring is the same for seeds across the groups (density and distance categories) being compared. A ratio greater than 1 indicates increased risk and a ratio less than 1 indicates less risk when compared to the reference category. For this analysis, we used the number of days between sampling occasions as the time variable. For the event variable, we coded the number of seeds at each seed station for each sampling occasion as ‘1’ when no viable seeds were present at a seed station or as ‘0’ when viable seeds were present. The Cox Proportional Hazards Model was built using the coxph() function and visualized using the ggforest() function from the {survival} and {survminer} packages (Therneau, 2023; R Core Team, 2021).

We employed a parametric approach to assess the influence of density, distance, and seed traits (length, weight, volume, and protection) on seed mortality resulting from vertebrate predation. All seed trait predictors, except for seed protection, were continuous variables. Seed protection was an ordered categorical variable with three categories: 'soft' (capable of being broken by fingernail), 'hard' (resistant to breakage by fingernail), and 'stone' (seeds with true stones). Density and distance were both ordered categorical variables, each with three categories, as previously mentioned. The response variable, seed mortality from vertebrate predation, was binary: labeled 'yes' for seeds predated upon by vertebrates, and 'no' for seeds that were not predated. Seeds moved away and subsequently lost were excluded due to their unknown fate.

To explore the influence of predictors on the response variable, we used generalized linear mixed-effects models with the glmer() function, from the package {lme4} (Bates et al., 2015), applying a 'binomial' error family and a 'logit' link function. The fixed effects included seed weight (g), seed length (mm), seed volume (cubic millimeters), seed protection (soft, hard, stone), density (low, medium, high), and distance (0m, 25m, 50m). Additionally, we integrated plant species as a random effect to account for potential species-specific variability. Given the substantial correlation among continuous seed trait variables, we avoided simultaneous inclusion within a single model to prevent collinearity issues, which could prevent model convergence or yield unreliable effect size estimates. Furthermore, we constructed models incorporating interaction terms: {density x distance}, {seed protection x seed weight}, {seed protection x seed length}, and {seed protection x seed volume}.

Model comparison was performed through the use of Akaike’s Information Criterion corrected for sample size (AICc) using the AICctab() function from the package {bbmle} (R Core Team, 2021). Notably, model coefficients were provided on the log-odds (logit) scale. To facilitate interpretation, we back transformed both the predicted values and the confidence interval boundaries from the logit scale to the original scale using the plogis() function.

Finally we used a parametric approach to assess the influence of density, distance, and seed traits (length, weight, volume, and protection) on the odds of a hoarder caching a seed rather than consuming it. The hoarding species included were Malayan porcupine, three-striped ground squirrel, tufted ground squirrel, and rats. The response variable, indicating the behavioral choice between eating or caching, was modeled as a binomial variable. To explore the impact of these predictors on the response variable, we employed generalized linear mixed-effects models with the glmer() function. These models utilized a 'binomial' error family and a 'logit' link function. Fixed effects included seed weight (g), seed length (mm), seed volume (cubic millimeters), seed protection (soft, hard, stone), density (low, medium, high), and distance (0m, 25m, 50m). Additionally, we incorporated plant species as a random effect to account for variability among species. Again, given the notable correlation among continuous seed trait variables, we decided against their simultaneous inclusion in a single model, as discussed earlier. We also constructed models featuring the following interactions: {density x distance}, {seed protection x seed weight}, {seed protection x seed length}, and {seed protection x seed volume}. Model comparison and the transformation of predictive values and confidence interval bounds followed the methods outlined previously.

Our findings revealed that the leading models (1st and 3rd) encompassed two highly correlated seed trait variables (weight and length), along with the predictor variable: distance (Table B3.3). We made the decision to exclude models that included length and volume (also highly correlated), while retaining models with weight to enhance the predictive performance of our best model. Notably, despite the enhanced predictive power, the effect sizes remained consistent. As a result, we are confident in our choice to exclude the trait variables (length and volume) from the models.

3.4 Results

3.4.1 Patterns of seed survival and mortality

Of the 963 seeds that we monitored, 33.7% (n=325) were preyed upon by vertebrates, 8.5% (n=82) by invertebrates, and 9.2% (n=89) were killed by fungus (Figure B3.1). Further, 9.5% (n=92) died at the seedling stage from herbivory (n=25), abiotic factors (n=56), and unknown causes (n=15). For 1.1% (n=11) of seeds, we could not ascertain the cause of death. While 11.3% (n=109) were recorded as alive at the end of the study, 26.4% (n=255) of seeds were lost after removal, and their ultimate fate was not known to us (Figure B3.1). Thus, we were able to successfully track the fate of 708 seeds accounting for 73.5% of sampled seeds.

At least 240 (24.9% of seeds) germination events were recorded, of which 43.7% (n=105) transitioned into the seedling stage, of which 12.3% (n=13) were alive at the end of our study. Seedling mortality primarily resulted from abiotic factors (60.8%, i.e., 56 out of 92 deceased seedlings), evident through wilting and absence of herbivory signs (leaf predation). Additionally, 27.1% of seedlings were killed by herbivory, initially marked by leaf predation, and later by the retrieval of completely chewed tags attached to seedlings at their establishment site.

Out of the 240 recorded germination events, 71 seeds (29.5%) were from stations under the parent plant, while 85 seeds (35.4%) and 84 seeds (35%) belonged to stations 25 m and 50 m away from the parent plant, respectively. Among these germination events, 84.2% (n=202) occurred at seed stations, and the rest at caching sites.

At the time of germination 86.6% (n=208) of the 240 seeds were intact, while 6.2% (n=15) had fungus, 4.1% (n=10) showed insect activity, and 2.9% (n=7, all belonging to the genus *Willughbeia*) had been partially eaten (Figure B3.2 panel B). Germination was observed in

13 plant species, and *Willughbeia* sp. 3 (n=70) and *Strychnos* sp. 2 (n=52) accounted for 50.8% of germination events (Figure B3.2 panel B).

Time to germination varied from 2 days (*Strychnos* sp. *2*, n=1) to 99 days (*Dracontomelon costatum*, n=2) with a mean of 14.5 days (SD=12.7) (Figure B3.2 panel A). Of the 336 soft-coated seeds, germination was observed in 29.4% (n=99), while 28.5% (n=138) of 483 hard-coated seeds, and 2% (n=3) of 144 stony-coated seeds germinated (Figure B3.2 panel A).

Of the 69 germinated seeds that succumbed to predation, 36.2% (n=25), 36.2% (n=25), and 27.5% (n=19) were killed by vertebrates, invertebrates, and fungi respectively (Figure B3.2 panel C). Additionally, 38.3% (n=72) of germinated seeds died at the seedling stage, 8.7% (n=21) were removed by rats (n=6) and unknown vertebrates (n=15) and thereafter lost, and 21.2% (n=51) were alive and included 13 seedlings, 36 germinated seeds, and 2 germinated seeds with insect activity. For 2.9% (n=7) of the germinated seeds we could not ascertain the cause of death.

A total of 109 seeds were recorded as alive at the end of the study, 77% (n=84) at the seed stations and 22.9% (n=25) at caching sites. Highest number of survivors, 49.5% (n=54), were counted from seed stations that were furthest away or 50m from the parent plant, while 32.1% (n=35) and 18.3% (n=20) were counted at stations that were 25m away and below the parent plant respectively.

Of the 109 survivors, 4.5% (n=5), 36.6% (n=40), and 58.7%(n=64) were soft-, hard-, and stony-coated seeds. These seeds belonged to seven plant species (representing four genera and families) and included seedlings (11.9%, n=13), germinated seeds (34.8%, n=38), intact seeds (19.2%, n=21), seeds with insect activity (22.1%, n=24), seeds with insect activity and fungus

(9.1%, n=10), germinated seeds with insect activity (1.8%, n=2), and seeds with fungus (0.9%, n=1) (Figure B3.3).

Around 56.8% (n=62) of survivors belonged to the woody climber *Strychnos* sp. 2, 62.9% of which had germinated and 11.2% had emerged into seedlings (Figure B3.3). It is important to note that we began sampling this species of *Strychnos* only in November 2020, towards the end of the study period. *Canarium* sp. 2, which had the largest seeds with the hardest seed protective layer among the sampled species, accounted for 27.5% (n=30) of seeds that survived, however 73.3 % (n=22) of them showed signs of insect activity (Figure B3.3). Due to their stony shells, it was difficult to ascertain the extent of insect damage without breaking open the seeds.

As some of our tagged *Canarium* sp. 2 seeds were still being cached and re-cached by vertebrate predators, we chose not to remove those seeds for further examination. Instead, we collected over a dozen *Canarium* sp. 2 seeds from the forest floor that showed similar signs of insect damage. We stored them in airtight containers for a week to check for invertebrates exiting the seeds. At the end of the week, when no insects were observed in the containers, we broke open the seeds to see if they were still viable. All seeds were dead; empty, with no traces of the endosperm or the embryo visible.

However, based on this finding alone, we cannot be certain that 22 of the 30 seeds belonging to *Canarium* sp. 2 were dead as well. This uncertainty can be attributed to two main factors: a) the active movement of some of these seeds by seed predators, and b) the potential for the seeds we gathered from the forest floor to have experienced longer exposure times compared to the seeds we tracked.

3.4.2 Seed survival over time as a function of density and distance

Results from the Cox Proportional Hazard model show that seeds at seed stations that are 25m away and 50m away from the parent plant had a hazard ratio of 0.76 (95% CI = 0.51-1.1) and 0.71 (95% CI = 0.48-1.0) respectively. In other words, seed stations away from the parent plant had a lower risk of complete seed loss when compared to seed stations under the crown of the parent plant (Figure 3.2). Next, seed stations with medium and low densities of seeds faced a significantly higher risk of complete seed loss with a hazard ratio of 2.04 (95% CI = 1.35-3.1) and 3.17 (95% CI = 2.09-4.8) respectively, when compared to seed stations with high densities of seeds (Figure 3.2).

3.4.3 Seed predator network

The bipartite seed predator network diagram utilizes the width of the axes (or the height of the rectangles, Figure 3.3) to portray the proportional abundance of predators (right) and plants (left). This height accurately represents the level of representation of each species, known as a node, within the context of the studied interaction—seed predation. On the predator axis, the width of a species corresponds to the total number of seeds preyed upon by all individuals of that predatory species. Conversely, on the plant axis, the width of a species denotes the total number of seeds preyed upon from all individuals of that plant species (Figure 3.3).

Our findings reveal distinctive patterns. Among the known predators, rats, followed by bearded pigs, invertebrates, and fungi, were responsible for higher proportions of seed predation or removal. On the plant axis, *Willughbeia* sp. 1, followed by *Diospyros* sp. and *Irvingia malayana*, experienced higher levels of seed predation and removal (Figure 3.3). It is important to note that rats, invertebrates, and fungi encompass groups with multiple species. As a result, it is probable that the species within these groups have a reduced level of representation at the species level, with bearded pigs potentially displaying a heightened level of representation on the predator axis if all taxa could have been identified to species.

In a bipartite network, the degree index, or the number of links, indicates the number of plant species the seed predator interacts with. In this seed predator network, rats were linked to 12 plant species, while invertebrates and bearded pigs had 10 and 9 links respectively (Figure 3.3; Table 3.2). The tufted ground squirrel, a specialist predator, had three links: two with plants that had stony-coated seeds, and one with a plant with hard-coated seeds. The width of a link signifies the strength index, a weighted metric based on the relative frequency of interactions between the linked predator and plant species. High strength indices imply targeted, intensive interactions. Among known predators, interactions of rats (strength = 3.37), pigs (strength = 2.65), and invertebrates (strength = 2.22) with their associated plant species were notably stronger when compared to other forms of predation (Table 3.2).

3.4.4 Patterns of seed predation

Seed predators: Bearded pigs were responsible for the highest amount of vertebrate seed predation (n=153 seeds; or 47% of seeds killed by vertebrates), followed by rats (n=59; 18.1% of seeds killed by vertebrates) (Figure B3.4). Tufted ground squirrels (n=24), three-striped ground squirrels (n=18), red langurs (n=16), mouse deer (n=13), and Bornean crested firebacks (n=5) together were responsible for 23.3% of predation by vertebrates. Around 11% (n=37) of seeds were killed by vertebrates whose identity could not be ascertained (Figure B3.4). A total of 89 seeds died from fungus of which 80.8% (n=72) belonged to the *Diospyros* sp. under study, 16.8% (n=15) to *Strychnos* sp. 2, and one seed each from *Irvingia malayana* and *Xanthophyllum* sp. (Figure B3.4). Of the 82 seeds that were killed by insects, ants were responsible for 53.6% (n=44) of seed mortality, while beetles (n=3 seeds), worms (n=3 seeds), and unidentified larvae (n=1 seed) together accounted for 8.5%. The remaining 37.8% seeds (n=31 of 82) were killed by unknown invertebrates (Figure B3.4).

Seed predators and seed density: A larger proportion of seeds belonging to high and medium density seed stations were killed by bearded pigs compared to other predators (Figure B3.5 panel A). Of the 309 seeds killed from high density seed stations, 30% (n=93), 18.7% (n=58), 11.9% (n=37), and 8.4% (n=26) were killed by bearded pigs, fungi, rats, and ants respectively (Figure B3.5 panel A). Of the 154 seeds killed from medium density seed stations, 34.4% (n=53), 14.9% (n=23), 9.7% (n=15), and 8.4% (n=13) were killed by bearded pigs, fungi, rats, and ants respectively (Figure B3.5 panel A). Of the 38 seeds killed from low density seed stations, 21% (n=8), 18.4% (n=7), 18.4% (n=7), and 13.1% (n=5) were killed by fungi, bearded pigs, rats, and ants respectively (Figure B3.5 panel A).

Seed predators and distance of seed/s from parent plant: A larger proportion of seeds belonging to seed stations located 50 m away from the parent plant and those located below the parent plant were killed by bearded pigs compared to other predators (Figure B3.5 panel B). Of the 141 seeds killed from seed stations 50 m away, bearded pigs killed 41.8% (n=59), and 17.7% (n=25) were killed by fungi. Bearded pigs were responsible for 30.6% of 215 seeds killed from seed stations located under the parent plant, while 14.4% (n=31) and 13.4% (n=29) were killed by rats and fungi respectively (Figure B3.5 panel B). Fungi killed a larger proportion of seeds from seed stations located 25 m away from the parent plant. Of the 145 seeds killed from seed stations located 25 m away from the parent plant, 24.1% (n=35), and 19.3% (n=28) were killed by fungi and bearded pigs respectively (Figure B3.5 panel B).

Seed predators and seed protection: Of the 138 soft-coated seeds killed, bearded pigs killed 57% (n=77) (Figure B3.5 panel C). A majority of the soft-coated seeds (31.1%; n=43) killed belonged to *Willughbeia* sp. 1 and were killed by bearded pigs (n=24), mouse deer (n=11), Bornean crested firebacks (n=4), and unknown vertebrates (n=4). Thirty-five (25.3%) soft-coated seeds killed belonged to *Madhuca* sp., a majority of which were killed by bearded pigs (n=31) (Figure B3.6 panel A; Table B3.1).

Of the 305 hard-coated seeds killed, fungi killed 29.3% (n=89) of seeds, of which 80.8% (n=72) belonged to *Diospyros* sp., and bearded pigs killed 22.7% (n=69), followed by ants (14.5%; n=44) and rats (12.2%; n=37) (Figure B3.5 panel C). With respect to stony-coated seeds, 63 of 64 seeds that were killed, were preyed upon by vertebrates: tufted ground squirrels (36.5%; n=23), rats (17.4%; n=11), three-striped ground squirrels (15.8%; n=10), pigs (11.1%; n=7), while the rest were killed by unknown vertebrates (Figure B3.5 panel C).

Of the stony-coated seeds killed, *Dracontomelon costatum*, the smallest stony-coated species, accounted for 26.5% (n=17), a majority of which (64.7%; n=11) were killed by tufted ground squirrels. Next, *Canarium* sp. 2, the largest of the stony-coated seeds, accounted for 26.5% (n=17) of stony-coated seeds that were killed, and a majority of which (70.5%; n=12) were killed by tufted ground squirrels. The intermediate sized *Canarium* sp. 1 lost 46.0% (n=29) to vertebrate predation, and these seeds were preyed upon by three-striped ground squirrels (31%; n=9), pigs (20.6%; n=6), rats (20.6%; n=6), and the rest by unknown vertebrates (Figure B3.6 panel A; Table B3.1).

Smaller rodents moved a greater proportion of stony-coated seeds away than they ate immediately (Figure B3.6 panel B). These seeds were cached or could not be located. Of the 31 *Dracontomelon costatum* seeds moved away from the seed station, rats were responsible for

74.1% (n=23) of seeds that were moved (Figure B3.6 panel B). A total of 27 seeds of the intermediate-sized *Canarium* sp. 1 were moved away, and three-striped ground squirrels moved 74% (n=20) of them (Figure B3.6 panel B). Of the 28 seeds from the large sized *Canarium* sp. 2, tufted ground squirrels moved 53.6% (n=15) and three-striped ground squirrels moved 46.4% (n=13) (Figure B3.6 panel B).

3.4.5 Seeds removed and lost

Rats removed 95 seeds from seed stations (n=83) and from caches (n=12) which we could not locate thereafter, accounting for 37.2% of the lost seeds. An additional 144 seeds (56.4% of lost seeds) were removed by unknown vertebrates from seed stations (n=99) and caches (n=45). A total of 15 seeds (5.8% of lost seeds) were removed by unknown invertebrates from seed stations (n=1) and caches (n=14). A single seed removed by a three-striped ground squirrel from a seed station couldn't be located thereafter.

Among the 95 seeds removed by rats, 61% were soft-coated, belonging to *Willughbeia* sp. 1 (n=5), *Willughbeia* sp. 2 (n=22), *Willughbeia* sp. 3 (n=5), *Lansium domesticum* (n=20), and *Madhuca* sp. (n=6). Furthermore, 11.5% of the 95 seeds were hard-coated belonging to *Palquium* sp. (n=9), *Irvingia malayana* (n=1), and *Strychnos* sp. 2 (n=1). The remaining 27.3% were stony-coated seeds of *Dracontomelon costatum* (n=23) and *Canarium* sp. 1 (n=3).

Out of the 95 seeds, 24.2% (n=23), 42.1% (n=40), and 33.6% (n=32) were removed from beneath the parent plant, 25 meters away, and 50 meters away, respectively. Notably, 64.2% (n=61) of seeds removal by rats occurred at high-density seed stations, while 31.5% and 4.2% were from medium and low-density seed stations, respectively.

3.4.6 Factors affecting the probability of seed predation by vertebrates

Of the 22 generalized linear mixed-effects models that we compared, the model that included density, distance, and an interaction between them, emerged as the top model with 84% of the Akaike weight (Table B3.2). The results indicated that at high densities (reference level), the likelihood of seeds being killed by vertebrates when located 50 m away from the parent plant was low, with a predicted probability of 0.15 (SE = 0.05; 95% CI = 0.09 – 0.26), as compared to seeds located below the parent plant (reference level) (Figure 3.4). Similarly, for seeds located 25 m away from the parent plant, the likelihood of being killed by vertebrates was also low, with a predicted probability of 0.29 (SE = 0.09; 95% CI = 0.17 – 0.43), as compared to seeds located below the parent plant (Figure 3.4).

For the density variable, the results indicated that for seeds located under the tree (reference level), the likelihood of seeds being killed by vertebrates at medium densities was high, with a predicted probability of 0.74 (SE = 0.31; 95% CI = 0.55 – 0.86), in comparison to seeds at high densities (reference level) (Figure 3.4). Similarly, for seeds at lower densities, the likelihood of being killed by vertebrates was high, with a predicted probability of 0.77 (SE = 0.62; 95% CI = 0.41 – 0.94), when compared to seeds at high densities (reference level) (Figure 3.4).

Seeds at medium densities located 25 m away from the parent plant faced a lower likelihood of vertebrate predation, with a predicted probability of 0.23 (SE = 0.14; 95% CI = 0.08 – 0.50), in comparison to seeds located at high densities under the parent plant (reference level) (Figure 3.4). Similarly, seeds at low densities located 25 m away from the parent plant also experienced a reduced likelihood of vertebrate predation, with a predicted probability of 0.14 (SE = 0.16; 95% CI = 0.02 – 0.58), compared to seeds at high densities under the parent plant (reference level) (Figure 3.4). Seeds at medium and low densities located 50 m away from the parent plant faced a likelihood of vertebrate predation of 0.66 (SE = 0.38; 95% CI = 0.39-0.86) and 0.28 (SE = 0.30; 95% CI = 0.05-0.76), respectively, when compared to seeds at high densities under the parent plant (reference level) (Figure 3.4).

3.4.7 Seed caching

In this study we did not record any larder hoarding events. We located a total of 176 seeds at 176 primary caching sites. Among the cached seeds, 37.5% (n=66) were cached by rats, and 36.9% (n=65) by three-striped ground squirrels (Figure 3.5 panel A). The remaining 25.5% were cached by unknown invertebrates (n=19 seeds), tufted ground squirrels (n=15 seeds), unknown vertebrates (n=10 seeds), and a Malayan porcupine that cached a single seed (Figure 3.5 panel A).

The cached seeds represented 15 plant species, with the majority belonging to *Irvingia malayana* (18.2%; n=32), *Canarium* sp. 2 (16%; n=28), *Canarium* sp. 1 (13.1%; n=23), *Lansium domesticum* (10.8%; n=19), and *Dracontomelon costatum* (8.5%; n=15) (Figure 3.5 panel B).

With respect to seed protection, a substantial portion of the cached seeds were stony-coated (37.5%; n=66) that were cached by three-striped ground squirrels (n=33), rats (n=16), tufted ground squirrel (n=15), an unknown invertebrate (n=1), and an unknown vertebrate (n=1) (Figure 3.5 panel B). Hard-coated seeds (35.7%; n=63) were cached by three-striped ground squirrels (n=31), invertebrates (n=16), rats (n=12), unknown vertebrates (n=3), and Malayan porcupine (n=1). Soft-coated seeds (26.7%; n=47) were cached by rats (n=38), unknown vertebrates (n=6), invertebrates (n=2), and three-striped ground squirrels (n=1) (Figure 3.5 panel B).

Around 41.4% (n=73) of seeds were cached 1-5m away from the boundary of the seed station, by rats (n=32), three-striped ground squirrels (n=25), tufted ground squirrels (n=8), unknown vertebrates (n=6), and unknown invertebrates (n=2) (Figure 3.5 panel D). A total of 48 seeds (27.2%) were cached within a meter from the boundary of the seed station by rats (n=19), unknown invertebrates (n=17), three-striped ground squirrels (n=8), unknown vertebrates (n=3), and Malayan porcupine (n=1) (Figure 3.5 panel D).

Forty one seeds (23.2%) were cached 5-10m away from the boundary of the seed station by three-striped ground squirrels (n=23), rats (n=10), tufted ground squirrels (n=7), and an unknown vertebrate (n=1) (Figure 3.5 panel D). Eight seeds (4.5%) were cached 10-15m away from the boundary of the seed station by three-striped ground squirrels. Five seeds (2.8%) were cached 15-20 m away by rats (n=4) and a three-striped ground squirrel (n=1). One seed was cached beyond 20 m from the boundary of the seed station by a rat (Figure 3.5 panel D).

Seeds were found to be cached in a diverse range of substrates. Most seeds (43.1%, n=76) were buried under the top layer of soil, not deeper than 5cm (Figure 3.5 panel C). This caching behavior was observed in three-striped ground squirrels (n=47), tufted ground squirrels (n=13), rats (n=11), unknown vertebrates (n=3), as well by a Malayan porcupine and an unknown invertebrate that cached one seed each in this manner (Figure 3.5 panel C).

Another caching strategy involved burying seeds under leaf litter, accounting for 25.5% (n=45) of cached seeds. Rats (n=27), three-striped ground squirrels (n=11 seeds), and unknown vertebrates (n=7) were responsible for this behavior (Figure 3.5 panel C). A total of 21% (n=37) of the cached seeds were found in various locations, including atop leaf litter (n=17), within burrows (n=7), on the ground (n=4), atop logs (n=3), within logs (n=3), and under leaf litter atop logs (n=3). Eighteen seeds (10.2%) were buried deeper under soil, with a single seed placed between 5-10 cm under soil by a rat, and 17 seeds placed more than 10 cm under soil by invertebrates (Figure 3.5 panel C).

Seeds remained in primary caches for an average duration of 25.9 days (SD = 42.1; Min = 3; Max = 357) (Figure B3.7 panel A).

Twenty eight of the 176 cached seeds, belonging to *Canarium* sp. 2 (n=14), *Lansium domesticum* (n=4), *Dracontomelon constatum* (n=3), *Irvingia malayana* (n=2), *Canarium* sp. 1 (n=2), *Willughbeia* sp. 3 (n=1), *Strychnos* sp. 1 (n=1), and *Madhuca* sp. (n=1) (Figure B3.7 panel C), were moved to secondary cache locations by three-striped ground squirrels (n=12), unknown animals (n=9), rats (n=5), and tufted ground squirrels (n=2) (Figure B3.7 panel B). These seeds remained at the secondary cache locations for an average duration of 27.3 days (SD = 23.1; Min = 3; Max = 93) (Figure B3.7 panel A).

Six seeds belonging to *Canarium* sp. 2 were moved to tertiary caches by three-striped ground squirrels (n=5) and an unknown animal (n=1) (Figure B3.7 panel B). Seeds remained in tertiary caches for an average duration of 40 days (SD = 21.9; Min = 3; Max=75) (Figure B3.7 panel A). Three of six *Canarium* sp. 2 seeds were moved to a fourth caching location by three-striped ground squirrels, where they remained for at least 1-27 days by the end of the study (Figure B3.7 panel A).

Instances of theft from caches of different species were observed among three-striped ground squirrels, who took *Canarium* sp. 2 seeds from the primary caches of tufted ground squirrels. Out of the 12 seeds that three-striped ground squirrels moved from primary to secondary caches, 4 belonged to tufted ground squirrels. Rats moved 5 seeds from five different plant species, transferring them from primary to secondary caches. Among these seeds, *Irvingia malayana* and *Canarium* sp. 1 were pilfered from primary caches belonging to three-striped ground squirrels. Tufted ground squirrels, which moved 2 seeds between primary and secondary cache locations, did so from either their own caches or those of conspecifics. Additionally, unknown animals moved 9 seeds from primary caches that belonged to rats (n=5), three-striped ground squirrels (n=2), and unknown vertebrates (n=2), relocating them to secondary caches.

Finally, out of the 176 seeds that were cached, a total of 38.6% (n = 68) were moved and lost, 25% (n = 44) were preyed upon by vertebrates, 14.7% (n = 26) were killed by insects, 2 died from fungal attack, and in the case of 2 seeds, we couldn't ascertain the cause of death. The remaining 19.3% of seeds were still viable.

3.4.8 To eat or hoard: the influence of density, distance, and seed traits

Among the 12 generalized linear mixed-effects models we compared, the model featuring distance and seed weight as fixed effects emerged as the best model, accounting for 78% of the Akaike weight (Table B3.4). The findings revealed significant patterns. For seeds situated 25 m away from the parent plant, the likelihood of being cached by hoarders was notably high, with a predicted probability of 0.82 (SE = 0.29; 95% CI = 0.69 – 0.90) (Figure 3.6). This is in comparison to seeds positioned below the parent plant, which served as the reference level. Likewise, for seeds positioned 50 m away from the parent plant, the likelihood of being cached by hoarders was significantly high, with a predicted probability of 0.81 (SE = 0.37; 95% CI = 0.63 – 0.91), when compared with seeds located below the parent plant (Figure 3.6). Furthermore, each unit increase in seed weight led to a significantly higher likelihood of being cached by hoarders, with a predicted probability of 0.85 (SE = 0.55; 95% CI = 0.61-0.95) (Figure 3.6).

3.5 Discussion

In this study, we successfully monitored the fate of 708 seeds, representing 73.5% of the sampled seeds. These seeds originated from 20 individual plants encompassing 15 large-seeded species. The seed predator network for the large-seeded plants we examined includes ungulates, a primate, a bird, rodents, invertebrates, and fungi. It is worth noting that the actual number of species is likely higher than presented here (12 including species and groups), as our ability to identify rodents, invertebrates, and fungi at the species level was limited.

At the end of the study, only 15% of the tracked seeds remained alive, with approximately 2% progressing to the seedling stage. Survival was notably higher in seed stations away from parent plants. Overall, vertebrate predation posed the greatest risk to seed survival during the seed stage, while abiotic factors were more important during the seedling stage.

3.5.1 Density- and distance dependent seed predation

Our seed survival analysis revealed a higher risk of seed loss at intermediate/lower densities compared to higher densities. The results from our generalized linear mixed-model analysis broadly supported these trends, with certain distinctions. Predictive probabilities derived from our best model indicated that seeds at intermediate/lower densities faced a greater risk of vertebrate predation under parent plants, compared to those at high densities. While not statistically significant, this suggests a potential positive density-dependence effect, possibly stemming from seed escape due to predator satiation in periods of or regions with high local seed densities (Kelly and Sork, 2002), such as beneath the parent plant.

In Southeast Asian Dipterocarp-dominated forests, synchronized mast fruiting events lead to acute periods of hyperabundant resources that satiate predators before the seed crop is exhausted (Blundell and Peart, 2004; Janzen, 1974). As a result, a proportion of seeds under parent plants and conspecifics escape predation, resulting in positive density-dependence. However, it has been pointed out that predator satiation may not necessarily be the driving factor behind enhanced survival near conspecifics (Curran and Leighton, 2000). Additionally, an examination of patterns of density-dependence across sites in Borneo shows high variability.

Blundell and Peart (2004) noted that initial positive density-dependence in seedlings can shift over time to Janzen-Connell patterns (negative density-dependence), while patterns have also been shown to vary across space (Bagchi et al., 2011). Bagchi et al., (2011), in their examination of patterns of seedling mortality during a non-mast year, observed that at a smaller scale, high seedling mortality near conspecifics aligns with Janzen-Connell predictions. However, when examined at a larger scale, higher seedling survival in areas of high conspecific densities indicates positive density-dependence (Bagchi et al., 2011). In contrast, consistent Janzen-Connell patterns in seedling mortality across scales have also been noted (Webb and Peart, 1999), and others have found no effects of distance or density on seedling mortality (Itoh et al., 1995). The observed variations in density-dependence can be attributed to factors including, but not limited to, environmental variation, resource availability, predator dynamics and behavior, and the specific plant life stage under assessment

In contrast to density-dependent patterns, our findings revealed distance-dependent vertebrate predation, aligning with the predictions of the Janzen-Connell hypothesis. Seeds in high-density clusters faced significantly lower odds of vertebrate predation at greater distances from the parent compared to when situated beneath the parent plant's canopy. However, evidence regarding distance-dependent seed predation within regions inhabited by diverse groups of mammalian seed predators has yielded mixed outcomes. Mammalian predators with high mobility and broad diets can alter seed distribution both nearby and farther from parent plants (Krishnan et al., 2022). Consequently, the risk of predation might not necessarily decrease with increasing distance.

Furthermore, vertebrate predators, characterized by differences in body size, movement patterns, and behavior, can variably influence seed mortality and survival (Hautier et al., 2010). In Borneo, Hautier et al., (2010) observed that large-bodied generalist predators, such as bearded pigs, reduced the survival of conspecific and heterospecific seeds indiscriminately, possibly negating the advantage of heterospecific recruitment. Conversely, small generalist species like rodents exhibited higher predation rates on conspecific seeds at the parent plant. In Afrotropical forests, Rosin and Poulsen (2016) noted that rodents removed more seeds from locations other than from beneath the parent plant.

Our study demonstrated that bearded pigs accounted for a higher proportion of seed mortality at more distant locations and beneath the parent plant, particularly at higher density seed stations. They also caused a greater number of seed deaths at intermediate distances compared to other vertebrates, although fewer than fungal predators. Rats exhibited similar proportions of seed predation across distances. Intriguingly, contrary to expectations, invertebrates and fungi killed more seeds at intermediate and greater distances compared to beneath the parent plant. Greater levels of seed predation away from parents by invertebrates (Krishnan et al., 2022), or distance-independent seed predation by invertebrates (Notman and Villegas, 2005), have been observed elsewhere. Fungal predation at our location was strongly skewed towards a single *Diospyros* species, indicating that it might not accurately represent the extent or patterns of mortality induced by fungi.

Thus, while our results may indicate positive density- and distance-dependent patterns, the underlying factors remain unclear based on our dataset. Further exploration is warranted to gain a deeper understanding of these dynamics.

Further, it is worth noting that our generalized linear mixed models are based on confirmed vertebrate predation events alone and do not include seeds that were removed and lost that are routinely included in such analysis but have the potential to bias results (Comita et al., 2014). However, our counts may be underestimated due to potential vertebrate predation on some lost seeds

3.5.2 Importance of large-bodied generalist seed predators

In general, seed mortality caused by generalist vertebrate seed predators, such as pigs and rats, was significantly higher than mortality caused by other predators recorded in this study. The significance of generalist species as both pre- and post-dispersal predators (Hautier et al., 2010; Clark et al., 2012; Paine et al., 2016; Paine and Beck, 2007), as well as dispersers (Brewer and Rejmánek, 1999; Vander Wall et al., 2005; Hirsch et al., 2012; Jansen et al., 2012), who can partially compensate for the absence of primary dispersal agents (Jansen et al., 2012), has been previously emphasized. While their prominence within seed predator assemblages in disturbed and fragmented landscapes has been recognized (Gopal et al., 2021; Krishnan et al., 2022), our results, along with other studies (Beck et al., 2013; Clark et al., 2012; Curran and Leighton, 2000; Hautier et al., 2010), indicate that they might play a more significant role than specialists (Connell, 1971; Janzen, 1970) in influencing patterns of seed mortality, establishment, and subsequent plant community structure, even within relatively undisturbed forests. This suggests the need to reconsider their role (Larios et al., 2017).

In line with observations made at other tropical sites, our results report that a larger proportion of seeds were killed by vertebrates when compared to insects and fungal predators (Bagchi et al., 2011; Gopal et al., 2021; Holl and Lulow, 1997; Rosin and Poulsen, 2016). While bearded pigs interacted with seeds of nine plant species, rats as a group were linked to twelve plant species. Yet, considering the likelihood that the group 'rats' may include several species, at the species level bearded pigs may be responsible for higher amounts of predation.

A few studies have examined the role of bearded pigs in influencing dynamics, especially during the early life stages of plants within their native range. Previously, at our site, Curran and Leighton (2000) noted that bearded pigs consumed vast quantities of fruits and subsequently seeds. Even during synchronous mast fruiting events, they were observed depleting large proportions of the seed crop, particularly affecting species that fruited asynchronously. Bearded pigs were noted as efficient fruit and seed foragers, capable of detecting them even when scattered at low densities. Additionally, they displayed significantly shorter handling times (Curran and Leighton, 2000).

In Malaysian Borneo, Ickes et al., (2001) noted that, apart from potentially causing seed mortality, bearded pigs' soil rooting behavior influenced stem densities, species richness, and plant growth. More recently, Hautier et al., (2010) observed that while small rodent seed predators removed a greater number of conspecific seeds from high-density patches, bearded pigs were less selective, removing both conspecific and heterospecific seeds from patches with both high and low seed densities. Thus, their foraging efficiency, natural behavior, lack of selectivity, combined with their ability to cover longer distances, makes them particularly effective seed predators capable of significantly suppressing seedling establishment on a considerable scale (Curran et al., 1999; Curran and Leighton, 2000).

Other studies have noted the significant role of small- and medium-sized mammals, as opposed to large mammals, in driving patterns of plant community structure (Paine and Beck, 2007; Jansen et al., 2012; Paine et al., 2016). This difference may stem from variations in mammalian seed predator assemblages.

3.5.3 Seed predator behavior and seed traits

In general, pigs engaged in on-site feeding and spent extended periods foraging at and around seed stations. In contrast, rodents often transported seeds a short distance away, either caching them and returning soon after, or consuming them.

Rats removing a larger proportion of seeds than they consume onsite aligns with results from some studies. Sidhu and Datta (2015) noted that seed removal was more than four times greater than immediate predation, while Jansen et al., (2012) noted that scatter-hoarding rodents rapidly removed 71.8% of seeds being monitored. In contrast, in Central Kalimantan, rats ate more seeds at the seed stations in forest and non-forest sites, however rats in forests took away more seeds for consumption when compared to the non-forest rats (Blackham and Corlett, 2015). The decision to remove or eat at a site may be determined by several reasons: seed traits, predation risk, resource abundance, competition, among others (Lichti et al., 2017).

Our study was conducted during the inter-mast period when resources are scarce and scattered (Marshall et al., 2009). This potentially intensifies competition from conspecifics, as observed in other rodent species (Hopewell et al., 2008; Murray et al., 2006), and from large-bodied seed predators like bearded pigs, which can rapidly deplete resources upon discovering a patch (Curran and Leighton, 2000). Consequently, the imperative to swiftly relocate scarce resources to safer locations for later consumption (Hopewell et al., 2008) might outweigh the allocation of more time to on-site consumption, potentially contributing to the higher removal rates we observed. Moreover, considering that our seed stations were situated in relatively exposed locations (for ease of monitoring), the threat of predation cannot be discounted (Boone et al., 2021), particularly at our site, which still hosts a full range of predators, including five species of felids.

While the influence of seed traits on overall vertebrate predation might be less reliable, as indicated by our GLMM analysis, we did observe variations in seed predation behavior that is potentially linked to differences in seed traits, specifically size and protection.

Seed predators respond to various traits; however, post-dispersal seed predation, particularly by smaller mammals, has been strongly linked to seed size (Dylewski et al., 2020). While global patterns indicate a preference for the removal of intermediate-sized seeds by small mammals (Dylewski et al., 2020), selection at specific sites can be influenced by several factors, such as habitat type (Dylewski et al., 2020), predator body size, resource availability, nutrient content, handling time, competition, fear of predators, and more (Lichti et al., 2017).

We observed that the omnivorous bearded pigs consumed the highest proportion of soft-coated seeds, showing no (detectable) preference for seed size. In contrast, rats demonstrated a preference for removing soft-coated seeds, especially from species with smaller-sized seeds, such as *Willughbeia* sp. 2, *Willughbeia* sp. 3, and *Lansium domesticum*. While bearded pigs have been shown to exhibit less selectivity (Hautier et al., 2010), seed size has been demonstrated to especially influence rodent predation and removal (Dylewski et al., 2020, Lichti et al., 2017).

A preference for softer-coated smaller-sized seeds over larger ones by small mammals, including rodents, has been noted elsewhere (Gopal et al., 2021). Additionally, the effect of body size variations among rodents on the removal of seeds of different sizes has been observed.

Small murid rodents, likely constrained by their own body size, exhibit a preference for consuming and removing small-sized seeds, whereas larger-bodied rodents, such as porcupines, tend to prey on larger seeds (Rosin and Poulsen, 2018; Sidhu and Datta, 2015). Conversely, in other instances, a distinct preference by scatter-hoarders for larger seeds has been observed, often linked to their higher nutritional value (Wang and Chen, 2009). On the contrary, smaller seeds, which might offer relatively fewer benefits and demand less handling time, are consumed more quickly (Jansen et al., 2004; Lichti et al., 2017).

As previously mentioned, rodents at our site displayed a tendency to consume seeds away from the seed station. This made it more difficult to track immediate predation events, especially when they happened beyond the camera trap's field of view or when no seed remnants were left behind. Additionally, in line with observations from other sources (Sidhu and Datta, 2015), we noted rodents removing seed tags before taking the seed, which posed a challenge in definitively confirming seed consumption solely based on tag recovery.

Yet, drawing from existing knowledge on rodent seed predation, it is likely that soft-coated seeds were consumed faster in our study due to their perishable nature, vulnerability to infestation, and faster germination rates (as summarized by Lichti et al., 2017). Although we observed faster germination rates for soft-coated seeds compared to stony-coated seeds in our study, germination didn't consistently prevent removal or predation. Rodents are known to manipulate non-dormant seeds by pruning or removing embryos, slowing seed mass loss, and potentially extending dormancy for months, allowing longer storage (Cao et al., 2011; Jansen et al., 2006; Xiao et al., 2013). However, mortality was highest for soft-coated seeds, with only 4.5% remaining by the study's end.

The presence of large-sized seeds didn't consistently result in reduced seed predation by all small rodent species. On the contrary, *Canarium* sp. 2, the species with the largest sized seeds in our sample, was selectively preyed upon by medium- and small-bodied squirrel species. Interestingly, this seed was not consumed at all by the largest seed predator, the bearded pigs.

Seeds with the toughest seed coats, or true stones, were notably favored by squirrels and rats, either for consumption or removal. Rats frequently removed smaller *Dracontomelon costatum* seeds. Similarly, Sidhu and Datta (2015) also observed that seed protection acted as a deterrent against on-site predation by small murids, resulting in a greater removal of hard-coated small-sized seeds by rats.

While small-bodied three-striped ground squirrels removed a substantial portion of intermediate-sized *Canarium* sp. 1 seeds, all on-site predation of *Canarium* sp. 2 seeds was attributed to the specialist predator, the tufted ground squirrel. Seed architecture also appeared to influence access. While *Dracontomelon costatum* and *Canarium* sp. 1 seeds were accessible to pigs, rats, and the squirrel species, *Canarium* sp. 2 seeds seemed to necessitate specialist predators, like the tufted ground squirrel. Despite their large size and tough protection, *Canarium* sp. 1 seeds featured ridges along their length that potentially aided in breaking them open. In contrast, *Canarium* sp. 2 seeds were smooth and possibly more challenging to open

Low levels of predation on Canarium seeds, attributed to their hard seed coats, have been consistently reported from South and Southeast Asian forests (Ganesh and Davidar, 2005; Gopal et al., 2021; Kitamura and Yumoto, 2008; Sidhu and Datta, 2015). In all these instances, except for the case of Kitamura and Yumoto (2008), significantly lower levels of seed predation were reported. Seeds of *Canarium euphyllum* in Thailand, dispersed by hornbills, were actively removed by three species of rodents, including long-tailed rats and ground squirrels, also found at our site. The seeds were eventually preyed upon, and the delay in predation was attributed to the hardness of the seed coat (Kitamura and Yumoto, 2008). It should be noted that the hornbill-dispersed *C. euphyllum* is smaller in size compared to the Canarium sp. that we studied, which is primarily dispersed by deer as observed in Chapter 2 in this study. Blate et al. (1998) reported predation on Canarium seeds from our site to be between 0% and 0.5%.

Both Blate et al., (1998) and Marshall et al., (2021) observed that *Canarium* seeds at our site were mostly accessible to tufted ground squirrels, which possess extremely powerful jaws. Most sightings of this animal have been reported at fruiting *Canarium* trees (Blate et al., 1998; Marshall et al., 2021). Additionally, it was noted that since specialist predators like these are less abundant, *Canarium* seeds may not experience high mortality levels (Blate et al., 1998). However, Marshall et al., (2021) suggest that tufted ground squirrels have the capacity to significantly modify seed shadows of *Canarium* at our site.

In our study, we observed that three-striped ground squirrels were also capable of predation and secondary dispersal of these seeds, although we predominantly recorded caching, theft, and rechacing events by them. This discovery is significant, as it marks a novel finding; prior to our study, apart from few records of bearded pigs and giant squirrels no other mammal, apart from the tufted ground squirrel, had been reported to possess the capability to prey upon *Canarium* seeds (Blate et al., 1998; Marshall et al., 2021).

During our observations for another study involving fruit tree watches, we witnessed tufted ground squirrels and three-striped ground squirrels visiting the fruiting *Canarium* tree. However, the two squirrel species were never observed simultaneously, at least based on the area that we could visually monitor. Furthermore, tufted ground squirrels were often seen extracting seeds from the extremely tough *Canarium* fruits at remarkable speeds and consuming them onsite. They also regularly inspected seeds on the forest floor, demonstrating selectivity in choosing which ones to break open.

In contrast, three-striped ground squirrels were observed foraging on the ground, selecting a seed, and then scurrying off, sometimes returning shortly afterward, potentially having hoarded the seed. Additionally, we noted that bearded pigs interacted with *Canarium* sp. 2 fruits, but in all instances, the seeds were spat out intact. Similarly, when giant squirrels visited this species, they engaged in in-situ partial predation of the fruit itself, and the seeds were never consumed during our observations.

Finally, based on our observations, the role of insects in regulating *Canarium* populations could be more substantial than initially anticipated. With extended exposure times, insects might contribute to higher mortality rates, even for well-protected seeds. Specialized seed-boring beetles have been observed preying on seeds of *Mezzettia parviflora*, which possesses robust structural defenses against predation. These defenses necessitate substantial bite force typically from larger gapes, or require specialized predators, such as the observed beetles (Lucas et al., 2012). Additionally, Kitamura and Yunoto (2008) reported seed predation by borers on *Canarium euphyllum*. However, the authors noted that the swift removal of seeds by rodents could have mitigated the impact of insect predation (Kitamura and Yumoto, 2008).

In our study area, the ground beneath the canopy of the *Canarium* sp. 2 tree was covered with hundreds of seeds. None of the other plant species we studied exhibited comparable amounts of seed fall. In most cases, the seed or fruit crop on the ground was rapidly depleted. Upon examining several seeds from the ground, we found small burrows, potentially made by insects.

Certain species of granivorous beetles have demonstrated a differential preference for seeds with stronger and denser seed coats (Lundgren and Rosentrater, 2007). It is important to note that the seeds under investigation in those studies were considerably smaller than the *Canarium* seeds (Lundgren and Rosentrater, 2007). The researchers suggested that the intentional expenditure of energy to crack open robust seed coats might be balanced by the nutritional benefits gained. While they observed that larger seeds were not chosen, they noted that the strength of seed coats doesn't necessarily increase with the size of the seed (Lundgren and Rosentrater, 2007).

3.5.4 Seed caching by rodents

Our second GLMM analysis, in which we assessed the variables influencing rodents' choice to eat or cache seeds, revealed that seeds located further away from the parent plant had a higher probability of being cached. Our results suggest that isolated patches of seeds may be rapidly harvested upon discovery. Scatter-hoarding rodents are known to be efficient at searching wide areas and finding, retrieving, and pilfering scattered seeds that are often buried, using olfactory cues and spatial memory (Jansen et al., 2012; Wang et al., 2018). As a result, unburied scattered seeds are easily detected, making them susceptible to removal by granivorous predators. Both visually and olfactorily dependent predators can locate such seeds (Vander Wall, 1993).

In addition to distance, our model also suggested that heavier seeds were more likely to be cached than lighter ones. The removal and hoarding of larger seeds by scatter-hoarders have been extensively documented (Jansen et al., 2004; Jansen et al., 2012; Kuprewicz et al., 2019; Van der Meer et al., 2008; Wang and Chen, 2009; Xiao et al., 2005), and this behavior has been linked to factors such as higher nutritional value and the presence of secondary metabolites (Jansen et al., 2004; Wang and Chen, 2020; Wang and Yang, 2015; Xiao et al., 2006), the extension of handling time required for well-protected seeds (Lai et al., 2014), or the combined effect of multiple traits (Zhang et al., 2016), among others. Opposing trends have also been noted, with some studies reporting preferential consumption of highly sought-after, large, nutritious seeds, and contrasting patterns of caching for high-fiber, nutrient-poor seeds that tend to survive longer in caches (Yadok et al., 2020).

Smaller rodents, especially rats and three-striped ground squirrels, cached seeds most often. Tufted ground squirrels exclusively cached Canarium sp. 2 seeds. The composition of the scatter-hoarding community we report mirrors that observed in other Southeast Asian forests. For instance, Thailand (Kitamura and Yumoto, 2008), peninsular Malaysia (Yasuda et al., 2000), Indonesian Borneo (Blackham and Corlett, 2015; Blate et al., 1998; McConkey, 2005), and Malaysian Borneo (Van der Meer et al., 2008) reported common scatter-hoarders like spiny rats, long-tailed giant rats, and sunda giant rats. Ground squirrels were also noted as scatter-hoarders by Yasuda et al. (2000) and Kitamura and Yumoto (2008).

Our contribution lies in identifying the Malayan porcupine as an additional species. However, we only noted one porcupine caching instance, making it the only interaction with our tagged seeds throughout the study. This discovery is intriguing, considering porcupines are generally seen as predators (Rosin and Poulsen, 2017; Sidhu and Datta, 2015).

Caches contained a single seed, common among scatter hoarding rodents (Sidhu and Datta, 2015; Yasuda, 2000). Most caches were within 1-5 meters from seed stations, fewer over 10 meters. Distant caches were mostly made by three-striped ground squirrels followed by rats.

Rats more often cached seeds in leaf litter, while three-striped ground squirrels buried them in soil, consistent with observations made by Yasuda (2000).

Rats preferred soft seeds for caching, while three-striped ground squirrels favored hard, stony-coated seeds, mostly *Canarium* species. Kitamura and Yumoto (2008), observed ground squirrels caching *Canarium euphyllum* seeds for months. Some *Canarium* sp. 2 caches by three-striped ground squirrels at our site were 2-4 months old, with only one seed predation instance recorded. Rodents respond to seed dormancy, and tend to quickly move dormant seeds, take them farther, and re-cache them several times (Lichti et al., 2017). Our observations support this, as we noted frequent and repeated re-caching of *Canarium* sp. 2 seeds by three-striped ground squirrels. Furthermore, intense competition between conspecifics and other species like the tufted ground squirrel might also influence the frequent re-caching behavior of long-lasting resources (Jansen et al., 2004; Male and Smulders, 2007).

Sparse distribution, well-hidden seeds that are frequently moved have been proven to reduce cache pilferage (Dally et al., 2006; Male and Smulders, 2007; Vander Wall and Jenkins, 2003). Consequently, even if resources are initially stored in clusters, they are eventually redistributed, often resulting in low-density spatial patterns of seeds (Male and Smulders, 2017). This benefits both the cacher and the plants, as seeds travel longer distances away from conspecifics (Hirsch et al., 2012). Furthermore, certain isolated seeds that remain in optimal conditions and are not retrieved can experience an increased potential for germination and establishment (Jansen et al., 2012; Wang et al., 2014).

In summary, our study reveals a diverse array of predators and secondary dispersers, each exerting varying effects on seed fate. Our findings point to distance-dependent and potentially positive density-dependent seed predation patterns that merit further examination to comprehend the underlying causes. Moreover, our research underscores the substantial impact of vertebrate seed predators, particularly large- and small-bodied generalists, on seed mortality and survival dynamics. The results highlight the interplay between seed size and seed coat robustness, which variably influenced predation frequency, removal, and handling across different species. Lastly, our study suggests that small-bodied squirrels may play a crucial role in providing secondary dispersal services to plants facing limitations in dispersal agents.

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3.8 Tables and figures

Table 3.1. List of families and species, plant form, and number of individuals included in seed fate assessment. Seed protection was noted as soft (capable of being broken by fingernail), hard (resistant to breakage by fingernail), and stone (seeds with true stones).

Family	**Plant species**	**Avg seed weight (g)**	**Avg seed length (mm)**	**Avg seed width (mm)**	**Avg seed thickness (mm)**	**Seed protection/ Form**	**Number of individuals**	**Total number of seeds**
Burseraceae	*Canarium* sp.1	6.15	41.29	22.48	19.23	stone/tree	1	48
Burseraceae	*Canarium* sp.2	12.05	63.58	20.69	19.74	stone/tree	1	48
Ebenaceae	*Diospyros* sp.	2.02	25.69	11.92	8.40	hard/tree	2	99
Anacardiacea	*Dracontomelon costatum*	3.09	18.59	17.90	12.77	stone/tree	1	48
Irvingiaceae	*Irvingia malayana*	14.15	39.10	27.49	18.54	hard/tree	2	96
Meliaceae	*Lansium domesticum*	2.05	19.53	13.77	7.77	soft/tree	1	48
Sapotaceae	*Madhuca* sp.	2.19	27.08	14.37	12.04	soft/tree	1	48
Sapotaceae	*Palaquium* sp.	2.10	28.84	11.71	7.62	hard/tree	1	48
Moraceae	*Parartocarpus* sp.	2.48	19.66	16.43	13.05	hard/tree	1	48
Loganiaceae	*Strychnos* sp.1	0.53	16.56	10.31	4.80	hard/liana	1	48
Loganiaceae	*Strychnos* sp.2	0.92	19.05	11.65	6.57	hard/liana	2	96
Apocynaceae	*Willughbeia* sp. 1	8.45	36.45	19.36	16.32	soft/liana	2	96
Apocynaceae	*Willughbeia* sp. 2	2.45	22.90	12.63	8.75	soft/liana	1	48
Apocynaceae	*Willughbeia* sp. 3	1.83	20.10	14.64	8.91	soft/liana	2	96
Polygalaceae	*Xanthophyllum* sp.	1.33	14.64	11.60	7.45	hard/tree	1	48

Table 3.2. Degree and strength (species-level network indices) for individual seed predator species or groups within the bipartite seed-predator network of large-seeded plant species. Species degree indicates the number of plant species the seed predator interacts with, reflecting the diversity of partners each predator engages with. Species strength, on the other hand, sums up the dependencies between species, capturing the level of interdependence within the network. Interaction strength (b_{ij}) signifies the proportion of species *i*'s interactions with a specific partner (species *j*) in relation to the total registered interactions for species *i*.

Seed predator	**Scientific name**	**Degree**	**Strength**
unknown vertebrates	*na*	15	3.49
rats	*na*	12	3.37
invertebrates	*na*	10	2.22
Bearded pigs	*Sus barbatus*	9	2.65
three-striped ground squirrels	*Lariscus insignis*	5	0.45
fungus	*na*	4	1.28
tufted ground squirrels	*Rheithrosciurus macrotis*	3	0.95
mouse deer	*Tragulus napu, Tragulus kanchil*	2	0.17
Bornean crested firebacks	*Lophura ignita*	2	0.07
red langurs	*Presbytis rubicunda*	1	0.34

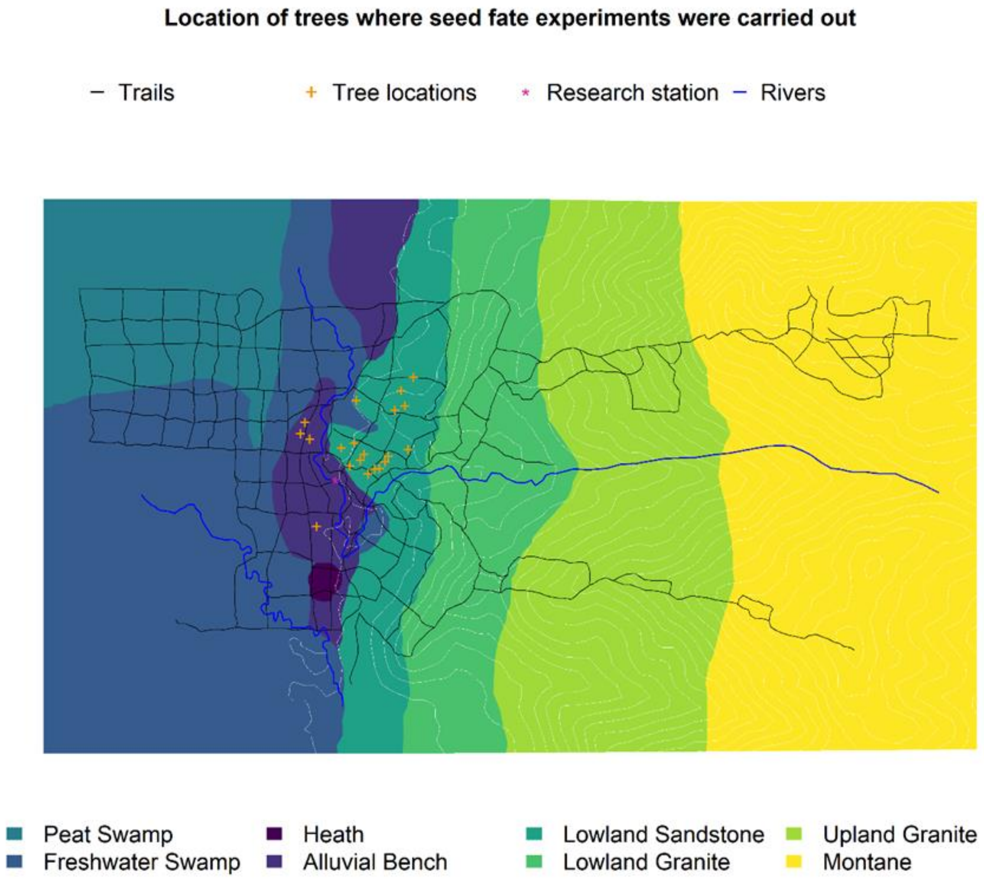

Figure 3.1. Map illustrating the trail system, forest classifications, and the geographical distribution of large-seeded plant species evaluated for post-dispersal seed fate within the Cabang Panti Research Site (CPRS).

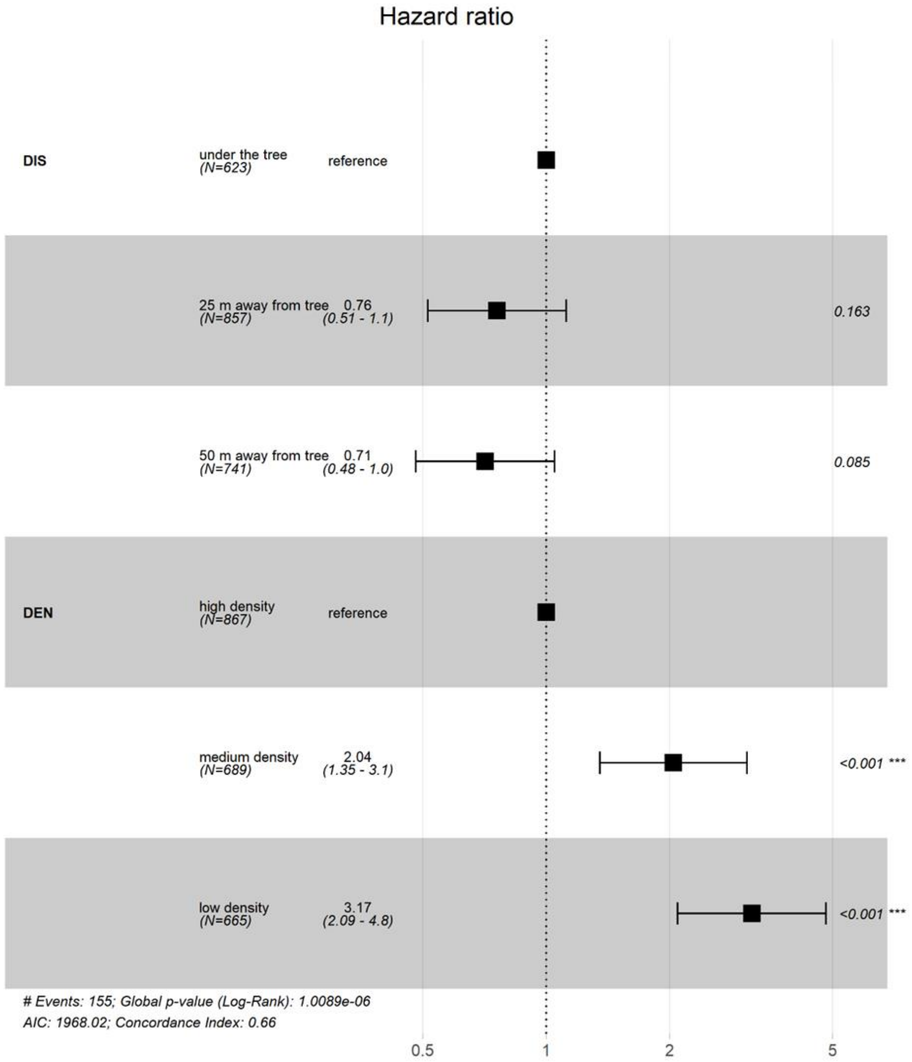

Figure 3.2. Hazard ratios along with their corresponding 95% confidence intervals and p-values for each variable incorporated in the model. Hazard ratios are calculated as exponentials of the coefficients. When the coefficient is positive or > 1, it signifies a higher risk for the study group compared to the reference group. Conversely, when the coefficient is negative or < 1, it indicates a lower risk for the study group compared to the reference group. A value of 1 signifies that the risk is equivalent for the study group in comparison to the reference group. In this context, "risk" pertains to total seed loss.

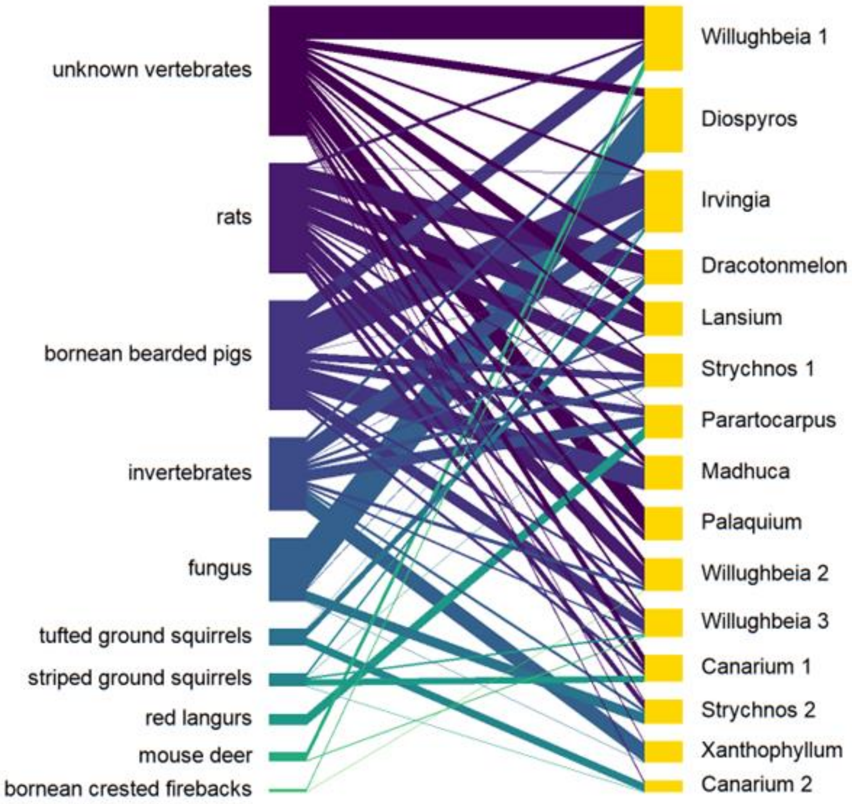

Figure 3.3. Bipartite network illustrating seed predation events recorded for each seed predator species or group across a range of large-seeded plant species in our study. The left axis, represented by purple to green bars, indicates seed predator species, while the right axis, shown as yellow bars, represents various large-seeded plant species. Links, in varying shades of purple to green, signify interactions where seed predators consumed seeds from corresponding plant species. Node width (height of rectangles) reflects species representation; on the predator axis, it indicates the total seeds consumed by that species, while on the plant axis, it denotes seeds preyed upon by the plant species. This visualization provides a comprehensive overview of ecological interactions in our study.

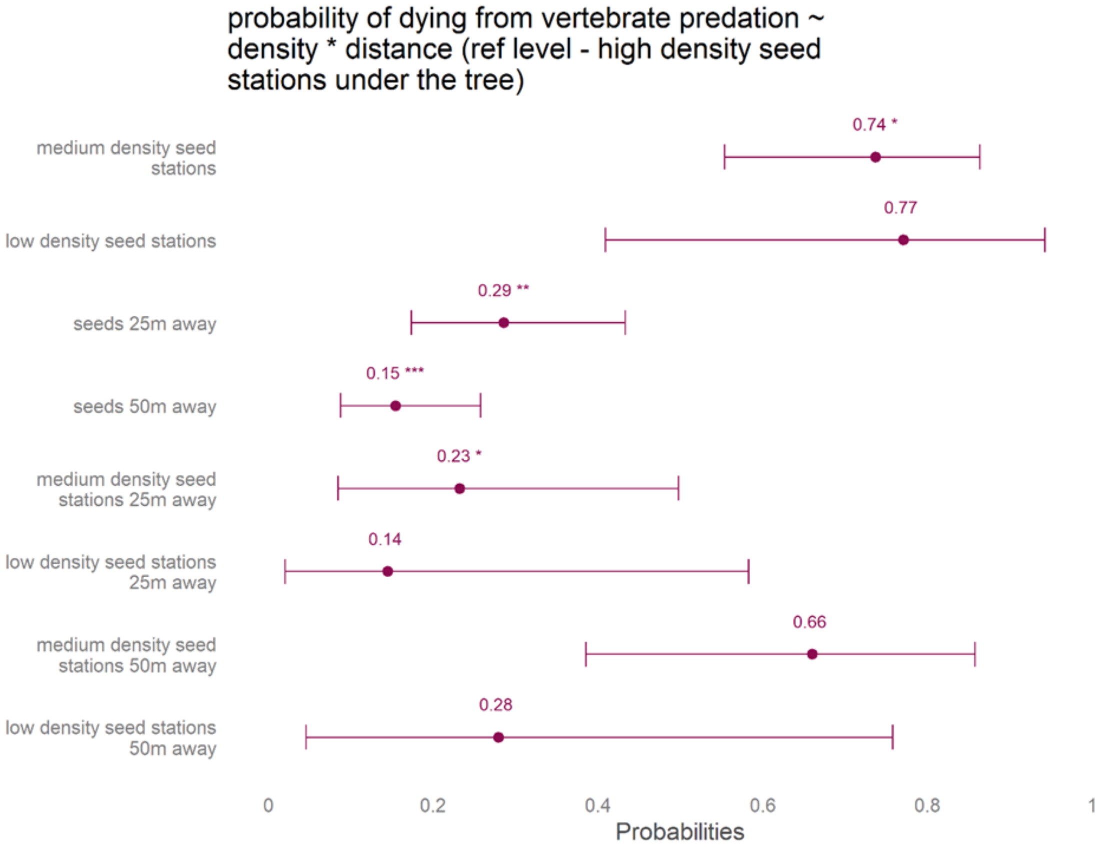

Figure 3.4. Probability of predation by vertebrates (a binary variable) in relation to the interaction between seed density (categorized as low=1 seed, medium=5 seeds, and high=10 seeds) and distance (categorized as 0m away from the parent plant, 25m, and 50m away). The coefficient plot represents the estimates from the best model, indicating the effect size and direction of density, distance, and their interaction. The predicted values and confidence interval boundaries, initially expressed in the log-odds (logit) scale, have been transformed back to their original scale using the plogis() function, with the exact values displayed above each bar. Points denote coefficient estimates, while error bars signify 95% confidence intervals.

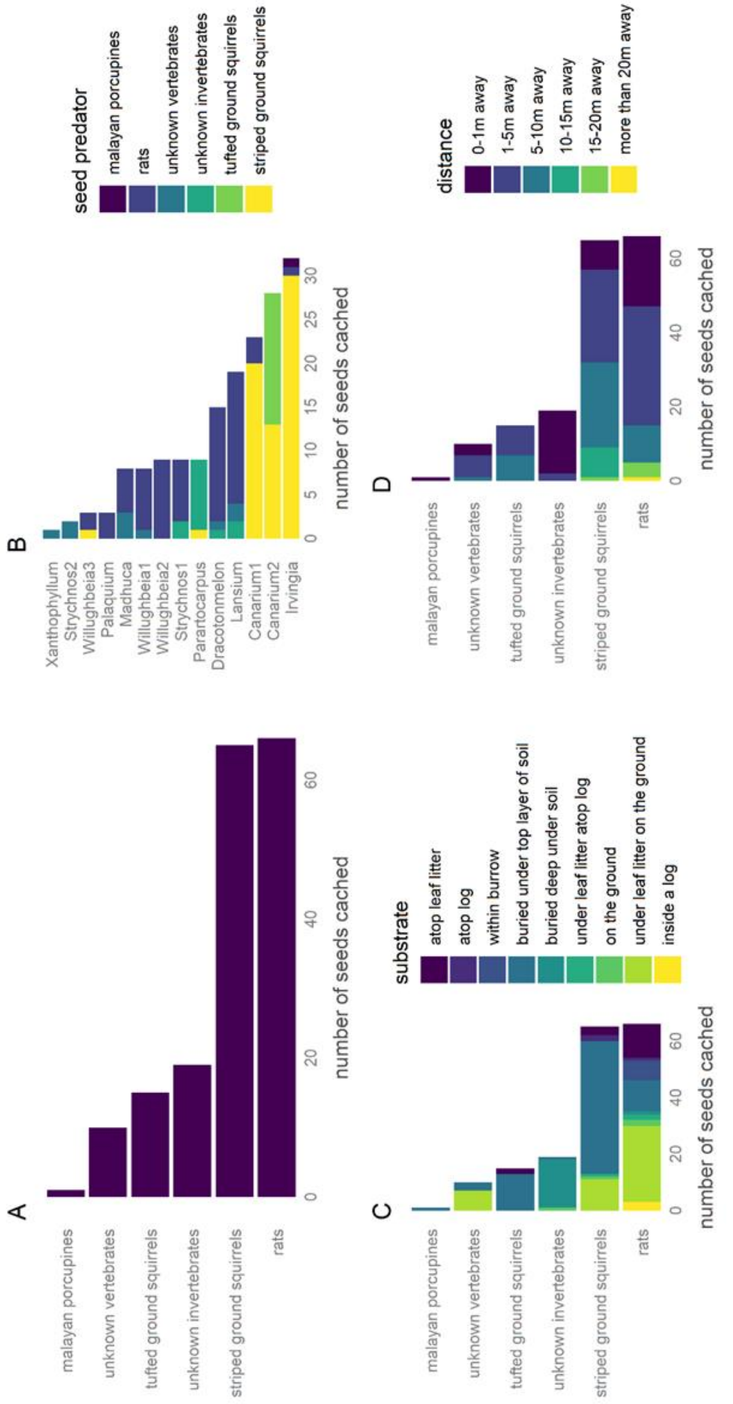

Figure 3.5. Overview of seed caching species and their behaviors. Panel A displays the total number of seeds cached by various animal species. Panel B illustrates the proportion of seeds cached by different animal species for each large-seeded plant species. Panel C illustrates the proportion of seeds cached by different animal species in various substrates. Panel D illustrates the proportion of seeds cached by different animal species at different distances from the source plant.

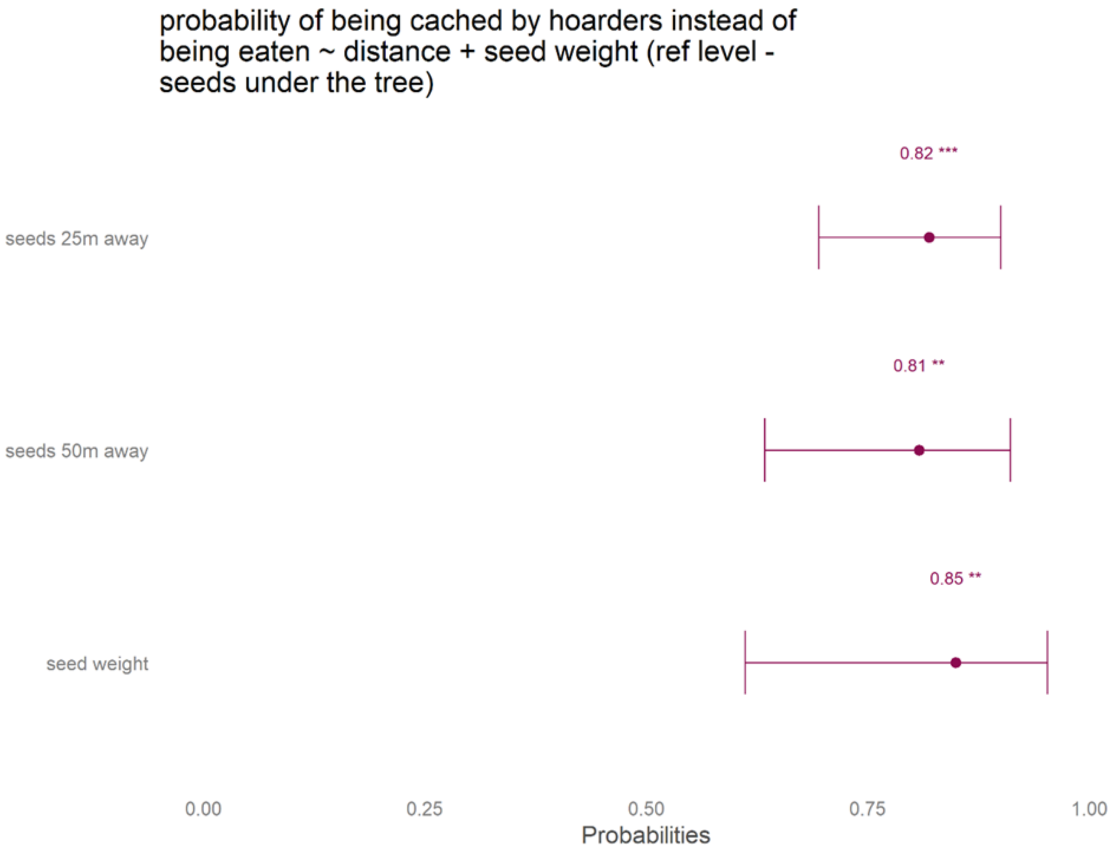

Figure 3.6. Probability of seed caching versus predation (a binary variable) by seed scatter hoarding species in relation to distance (categorized as 0m away from the parent plant, 25m, and 50m away) and seed weight (a continuous variable). The coefficient plot visually depicts the estimates obtained from the best model, providing insights into the effect size and direction of both distance and seed weight. Predicted values and confidence interval boundaries, initially expressed in the log-odds (logit) scale, have been transformed back to their original scale using the plogis() function, with the exact values displayed above each bar. Points denote coefficient estimates, while error bars signify 95% confidence intervals.

Chapter 4: Contemporary Hunting Practices in a Forest-Plantation Mosaic Landscape in West Kalimantan, Borneo, Indonesia

4.1 Abstract

In Indonesia, the expansion of labor-intensive plantations has transformed formerly forested landscapes into forest-plantation mosaics. This has led to changes in demography due to immigration, increased access to forest resources, and created new job opportunities with steady income. Within these contemporary landscapes, quantitative site-based assessments of hunting are largely lacking. Our study is the first systematic, multi-species assessment from Indonesian Borneo and focuses on threats from hunting to 33 species of mammals and birds. The main objectives of our study were to quantitatively examine the scale and motivations of and perceptions toward hunting. We collected in-depth data using a three-part structured questionnaire from 29 consenting Muslim Melayu hunters in villages adjacent to Gunung Palung National Park. Overall, our results showed that the odds of hunting larger animals (>1 kg) were higher than hunting smaller animals (<1 kg). While 26 species were hunted, religious prohibitions permitted eating meat from only a select few, including deer, mouse deer, porcupines, and gallinaceous birds. These species were noted as 'preferred,' hunted predominantly for food and infrequently for sale. Hunting prohibited species, including endangered species, occurred for other reasons such as pest control and, more rarely, for medicinal use and sale of animal parts. Our findings indicate that animal populations, especially ungulates, have critically declined, with the sambar (*Rusa unicolor*), the largest species in this landscape, being particularly affected. Most hunters attributed this decline to excessive hunting by both Melayu and non-Melayu hunters. While all respondents perceived hunting as risky, mainly due to physical danger, it was observed that many of them were not aware that hunting wild animals was illegal. Additionally, most hunters stated that they would discontinue and dissuade their children from hunting, mainly due to an effort-rewards imbalance. In conclusion, our study suggests that hunting disproportionately targets a few animal species in this area, and at least one species (*Rusa unicolor*) is possibly threatened with local extirpation.

4.2 Introduction

A silent threat continues to sweep through the tropics. Unsustainable hunting, one of the most urgent threats to wildlife (Ingram et al., 2021; Maxwell et al., 2016), affects a larger area across the tropics than deforestation and logging combined (Fa et al., 2002; Harrison, 2013; Ripple et al., 2016). When paired with land-use change, the joint impacts on biodiversity are far more critical (Gallego-Zamorano et al., 2020; Maxwell et al., 2016), even more than the impacts of climate change (Caro et al., 2022).

Hunting in tropical forests has evolved substantially over time. Increasing human population densities, advances in hunting technology, the commercial sale of wild meat, and improved infrastructure facilitating access to remote regions have contributed to a surge in hunting activities (Alves et al., 2018; Benitez-Lopez et al., 2017; Benitez-Lopez et al., 2019; Bennett and Robinson, 2000; Bennett et al., 2002; Corlett, 2007; Darimont et al., 2015; Fa et al., 2002; Harrison et al., 2016; Laurance et al., 2008; Robinson and Bennett, 2004; Rija et al., 2020; Wilkie et al., 2011). As a result, humans have emerged as global "super predators," hunting animals at rates 14 times higher than other predators (Darimont et al., 2015) for a variety of reasons beyond meeting basic subsistence needs (Alves and Van Vilet, 2018; Vliet et al., 2016).

This high rate of exploitation is unsustainable (Ingram et al., 2021; Ripple et al., 2016; Wilkie et al., 2011) and perpetuates the “half-empty” or “empty forest syndrome” (Corlett, 2007; Peres and Palacios, 2007; Redford, 1992; Redford and Feinsinger, 2001; Wilkie et al., 2011) where forests are depleted or devoid of species sensitive to hunting (Redford, 1992; Redford and Feinsinger, 2001).

While hunting occurs in various ecological, cultural, socio-economic, and political landscapes across the tropics (Alves et al., 2018), a common theme emerges: large animals are disproportionately targeted (Benitez-Lopez et al., 2019; Corlett, 2007; Fa et al., 2005; Fa et al., 2006; Fa and Brown, 2009; Harrison et al., 2016; Ingram et al., 2021; Peres and Palacios, 2007; Ripple et al., 2016). Due to their naturally low densities, slow life histories, limited recovery potential, and vulnerability to other stressors like habitat loss (Cardillo et al., 2005; Harrison et al., 2016), most large animals have either been extirpated or experienced significant population declines (Benitez-Lopez et al., 2017; Benitez-Lopez et al., 2019; Corlett, 2007; Rija et al., 2020). As a result, the proportion of tropical areas supporting large animals has drastically reduced (Harrison, 2011).

Southeast Asia, known for its rich biodiversity, experiences higher rates of hunting for subsistence and trade compared to other tropical regions (Gray et al., 2018; Krishnasamy and Zavagli, 2020; Minin et al., 2019; Nijman, 2010; Wilcove et al., 2013). This is attributed to high human densities, growing urban consumer markets, Southeast Asia's role as a major supplier to international markets, the utilization of a wider range of species than elsewhere in the tropics for various purposes beyond food, and to shrinking forests (Cardinale et al., 2012; Corlett, 2007; Duckworth et al., 2012; Fa and Brown, 2009; Vliet et al., 2016). Within this region, Indonesia has emerged as a wildlife trade hotspot (Bergin et al., 2018; Gomez et al., 2021; Harrison et al., 2011; Harrison et al., 2016; Heinrich et al., 2020; Krishnasamy and Zavagli, 2020; Lee et al., 2005; Luskin et al., 2014; Maulany et al., 2021; Natusch and Lyons, 2012; Nijman et al., 2012; Nijman et al., 2015; Nijman et al., 2017; Nijman et al., 2022; Shepherd et al., 2016; Sherman et al., 2022; TRAFFIC, 2008).

However, in-depth site-specific studies examining local hunting practices in Indonesia are limited in scope, having focused on one or a small number of animal species (Arobaya et al., 2021; Davis et al., 2013; Gomez et al., 2021; Laatung et al., 2019; Milner-Gulland and Clayton, 2002; Pangau-Adam et al., 2022; Sheherazade and Tsang, 2015; Struebig et al., 2007; Yudha et al., 2022) or on communities residing in forested landscapes with predominantly subsistence-based livelihoods and limited interaction with the cash economy (Alvard, 2000; Pangau-Adam et al., 2012; Wadley et al., 1997).

In the recent past, forested regions in Indonesia, especially in Kalimantan, have experienced rapid ecological changes driven by extensive forest conversion to plantations, mainly of oil palm (*Elaeis guineensis*), and to a lesser extent rubber (*Hevea brasiliensis*), as well as the growth of small-holder agriculture (Carlson et al., 2012; Carlson et al., 2013; Gaveau et al., 2014; Gaveau et al., 2016). These regions are now best described as a forest-plantation-farmland mosaic, with forests fragmented and reduced in size (Carlson et al., 2013; Sayer et al., 2012), making them more accessible, often leading to unsustainable levels of hunting (Harrison et al., 2016).

Rapid urbanization that usually follows land-use changes of this nature increases access to larger markets, increases connections between hunters and traders, and creates more opportunities for hunters to sell/supply wild meat and other animal parts. For example, in Papua, Indonesia, where subsistence hunting has existed for millennia, the establishment of oil palm plantations led to the emergence of commercial hunting practices (Pangau-Adam et al., 2012). Land conversion, and the resultant ecological changes, have also led to changes in hunting practices. As populations of pigs, considered agricultural pests, increased in a plantation-dominant landscape, they were hunted more heavily, shifting attention away from harvest-sensitive species (Luskin et al., 2014). Furthermore, as plantations require a larger labor force, their establishment often results in an influx of people into the area (Feintrenie et al., 2010; Rist et al., 2010). With more people and less forest, even small-scale subsistence hunting can potentially become unsustainable (Suarez and Zapata-Rios, 2019). Plantations do not, however, universally increase hunting rates. Because plantations offer more predictable sources of income, they can lead to rural livelihoods that are more market-based rather than subsistence-based (Feintrenie et al., 2010; Rist et al., 2010; Sayer et al., 2012), potentially alleviating pressures on wildlife when less time is allocated towards hunting. For example, both Bennett et al. (2000) and Luskin et al. (2014) found that people primarily working in plantations were less involved in hunting and consumed wild meat less frequently.

We have only begun exploring contemporary hunting practices within these vastly altered socio-ecological landscapes, and our understanding is currently limited to a handful of studies (Kurz et al., 2021; Luskin et al., 2014). Our study represents a modest effort to contribute to the small but crucial database of hunting practices within modern landscapes. In this study, we investigated hunting in a forest-plantation mosaic landscape in West Kalimantan, Borneo, Indonesia (see Figure 1). We assessed the frequency of hunting and the factors affecting hunting frequency. We explored motivations, traditional beliefs/practices, and perceptions associated with hunting. Additionally, we examined changes in hunting practices by comparing active hunters with former hunters. We assessed the conservation status of animals and investigated whether large animals face higher hunting risks, as observed elsewhere in the tropics.

Our study focused on assessing the threats posed by hunting to 33 species of mammals and large birds that frequently consume fruits and seeds. This selection complements our other efforts in understanding the significance of these fruit and seed-eating animal species for rainforest plants within the same landscape. Fruit and seed-eating animals play crucial roles in various interactions with plants, including mutualistic seed dispersal, essential for plant reproductive success (Simmons et al., 2018). Large-seeded plants rely heavily on a smaller number of mutualistic interactions with big frugivores like elephants, ungulates, primates, fruit bats, and large birds (Brodie et al., 2009; Kitamura et al., 2006; McConkey et al., 2018; Nuñez-Iturri and Howe, 2007; Sethi and Howe, 2012; Wheelwright, 1985) for effective dispersal (Kitamura et al., 2006; McConkey and Drake, 2015; Nathan and Muller-Landue, 2000; Traveset et al., 2007).

However, anthropogenic activities, particularly hunting-induced defaunation, have led to a decline in these interactions, negatively impacting the dispersal of large-seeded plants (Brodie et al., 2009; Kurten et al., 2015; Nunez-Iturri and Howe, 2007; Terborgh, 2013; Vanthomme, 2011; Wright et al., 2007). Comparing hunted and non-hunted areas has revealed lower species richness and densities of animal-dispersed plants in the hunted sites (Kurten et al., 2015; Nuñez-Iturri and Howe, 2007; Kurten, 2013). Long-term studies show that loss of frugivores has substantial effects on forest structure, affecting survival, seed recruitment, and tree diversity over time (Caughlin et al., 2015; Harrison et al., 2013). Therefore, by understanding current hunting practices, we determine the perceived conservation status of our focal animals and identify species that are especially threatened and may require targeted conservation attention.

To the best of our knowledge, ours is the first systematic, multi-species assessment of hunting practices from Indonesian Borneo.

4.3 Methods

4.3.1 Study area

We conducted this research in villages located within a forest-plantation mosaic habitat at the eastern boundary (Figure 4.1) of Gunung Palung National Park (GPNP), West Kalimantan, Indonesia, from March to May 2019. We selected this area after consulting with members of the GPNP office and wildlife crime informants from local conservation organizations. During these consultations, we identified villages at the national park boundary with prevalent hunting activity, suitable for our data collection. We made preliminary visits to several villages along the east and northeast park boundaries in March and early April 2019. We selected 4 sub-villages (dusuns) for data collection based on a) conversations with village chiefs during reconnaissance visits, b) proximity of the village to GPNP, and c) logistics and feasibility. The 4 sub-villages are administratively located within Kecamatan Sandai, one of 20 districts (kecamatan) that form the Ketapang Regency within the West Kalimantan Province of Indonesian Borneo. An additional village was included at a later point when one respondent consented to participating in the study.

4.3.2 Recruitment and participation of respondents

When we first arrived at each sub-village, we held several meetings with the village head and/or chief (*Kapala Desa* and/or *Kapala Dusun*), elders, priests (*imams*), teachers, and other prominent members of the community. During these meetings, we provided attendees with a) a detailed description of our study and b) the criteria for participation, including the requirement of verbal consent. Since hunting of many of our focal species is prohibited by law in Indonesia, and participation in our study could potentially be risky, we clearly outlined how we would maintain anonymity of respondents, thereby guaranteeing their safety from legal repercussions. Once we fully addressed all concerns and questions from attendees, we requested them to introduce us to potential respondents, including a) currently active hunters, b) recently active hunters (those who hunted in the last 10 years but do not hunt now), and c) formerly active hunters (those who used to hunt more than 10 years ago). These introductions resulted in the recruitment of at least one respondent. Subsequent recruitment of respondents occurred through referral sampling, where a former respondent introduced us to other potential respondents. While randomly sampling from an identified pool of potential respondents may ensure adequate representation of the community, we found, like Kurz et al. (2021), that referral sampling was more effective in recruiting respondents for our study, where trust-building was of paramount importance.

When we first approached potential respondents, we thoroughly briefed them about the study, the requirement of consent for participation, and the measures in place to mitigate risks associated with participation. We addressed all questions and concerns before inviting them to participate in our study. Several individuals did not consent to participate as they considered it risky; following this, we did not contact them again. Our statement for procuring verbal consent is included in Box C4.1. No monetary remuneration, gifts, or benefits were provided for participation in our study.

According to our protocol, we only recruited adults (18+ years old) for our study. In total, we collected in-depth data from 29 respondents during 25 interviews using a structured questionnaire (Box C4.2). The respondents included 25 currently and recently active hunters, and 4 formerly active hunters. The average time taken to administer the interview was 108 minutes.

While we intended to interview respondents individually, on some occasions (n=4), respondents were more comfortable being interviewed in pairs. At such times, responses were noted down independently for each respondent. All respondents were adult males. Although women in these communities do not hunt, they are responsible for the preparation of family meals that may include wild meat. Thus, while we did not actively seek out women respondents, on occasion (n=5), when spouses/mothers of hunters organically participated in the interview process, they were not discouraged. However, in all these instances, a single response was provided following a discussion between the male and female respondent, and therefore, a single response was recorded. All interviews were conducted at the residences of the respondents and on some occasions, other family members, neighbors, and/or friends were present despite our initial requests for discretion. On such occasions, we sought and recorded responses only from the interviewees.

All interviews were conducted in Bahasa Indonesia. Two interviewers (SN and KP) administered the questionnaire for each interview. As the principal investigator (SN) only had a working knowledge of Bahasa Indonesia, KP (an Indonesian student) served as a translator and subsequently helped with transcribing the interviews. Given the detailed nature of the interviews, they were recorded using a Dictaphone (Sony ICDPX370 Mono Digital Voice Recorder) and subsequently transcribed onto data sheets at a separate location. None of our participants expressed concern or showed discomfort about being recorded. Recording data in this manner a) minimized errors likely to occur when transcribing data during the interview, b) minimized interruptions to the conversation, and c) saved time; for example, transcribing a single interview took us a minimum of 2 hours.

To maintain respondent anonymity, no information on identification (name, address, signature, video, or photograph) was collected at any point.

Our interview protocol was approved by the University of Michigan's Institutional Review Board (IRB) for research involving human subjects (HUM00156618), and by RISTEK, Ministry of Research and Technology, Indonesia (Ref. No. 210/FRP/E5/Dit.KI/ll/2019).

4.3.3 Data collection

We used a three-part questionnaire to collect our data. In the first part, we collected basic information on demographics and socioeconomic status, including age, education level, occupation, sources of income, and land ownership. In the second part of our questionnaire, we collected detailed information on hunting practices using a set of 25 questions (Box C4.2). Broadly, we asked respondents about hunting frequency, motivation for hunting, nature of hunting, meat consumption and preferences, and perceptions/attitudes towards hunting.

In the third part, we collected data on threats from hunting to focal species. We collected this information for 26 frugivorous mammals and 7 species of frugivorous hornbills (Table C4.1). Here, we presented respondents with clear color photographs and detailed descriptions of each species. We resolved confusions regarding species identity by providing any additional natural history information known to us. However, many respondents failed to recognize or distinguish between some species (Table C4.2). No data were recorded for the respective species in such instances.

For species that were definitively recognized, we asked the respondent(s) if they hunted them. If they responded affirmatively, we further inquired if the species was preferentially hunted and what the main reasons were for hunting it. We define preferred animals as those that hunters reported actively seeking, as opposed to animals that they encountered opportunistically. For species that were preferentially or opportunistically hunted, we inquired about the motivations for hunting. When money was indicated as a motivation, we further inquired about the sale price. Additionally, we recorded reported sale prices, even when respondents didn't personally engage in selling but provided information based on sales by others or their own purchases. Finally, we asked respondents to help us assess the species' current status based on observed changes to populations over the last three decades (or an appropriate time frame for younger respondents). For this, we handed the respondent(s) the photograph and asked them to place it under one of five categories, with each category clearly indicated on a card: complete extirpation or extreme reduction, moderate reduction, no change, moderate increase, and extreme increase.

Most of our questions were closed questions that enabled us to collect readily quantifiable data. Responses to these questions were recorded either as categorical/ordered categorical data using predefined numerical codes, as binary data (yes/no; 0/1), or as discrete/continuous data. For open-ended questions, statements were recorded verbatim. Prior to commencing our study in March 2019, we tested our entire questionnaire on respondents (n=6) from two other villages outside our study area. This allowed us to revise/refine the questionnaire and add to our predefined categories where needed.

Although the slow loris was not among our focal species, it was mentioned by respondents in the context of cultural taboos. As a result, data on these species were incorporated into our subsequent discussions of results related to local taboos and prohibitions.

4.3.4 Data analysis

We used the R statistical and programming environment for data analysis and visualization (R Core Team, 2021).

We employed a range of data visualization techniques, including boxplots, histograms, and bar plots, to profile the interviewed hunters and analyze various demographic, socioeconomic, and hunting-related variables. To assess the conservation status of focal species, we summed all responses under each category depicting the current status of a species, for each focal species separately, and tabulated the resultant data.

Next, we used a parametric approach to model the frequency of hunting as a function of multiple predictors. How often a respondent hunted, an ordered categorical variable with 5 categories, was the response variable, while age (continuous), monthly household income (continuous), amount of land owned (continuous), possession of domestic animals (binary), number of years they have been hunting (discrete), how often wild meat is consumed (ordered categorical), how often wild meat is sold (ordered categorical), how often domestic meat is consumed (ordered categorical), and preference of wild or domestic meat (binary) were the predictor variables. To evaluate the effect of the predictors on the response variable, we built a series of 46 ordered logit models using function polr(). Within our models, we employed single predictors or combinations of up to two predictors. However, when we attempted to include additional predictors or interaction variables, we encountered errors and warnings primarily due to lack of model convergence. Consequently, we opted to restrict the number of predictors to ensure the stability and reliability of our models, leading us to exclude complex models from our analyses. Models were compared using Akaike's Information Criterion corrected for small samples (AICc)s. We plotted the predicted probabilities of each outcome based on our best model using plotting functions from the {effects} package.

Finally, to assess if large animals faced higher risks from hunting, we modeled hunting as a function of body size. Hunting, the response, was a binary variable indicating if the species was hunted or not. For our predictor, body size, we extracted body weight data for our focal species from the Phillips Field Guide to the Mammals of Borneo (Phillipps, 2016). We employed midpoints when a range was provided, or when there were variations in weights between males and females. We categorized this data into the following body weight categories: small animals (<1 kg) and large animals (1-10, 10-50, 50-100, and 100-250 kgs) before including the predictor in our model. To understand the effect of body size on whether a species was hunted or not, we built a generalized linear model using function glm(). We visualized effect sizes expressed as odds ratios, and their confidence intervals using plotting functions from {sjplot} (Hlavac, 2021).

4.4 Results

The results presented below are based on data collected from active and recently active hunters (n=25), unless stated otherwise, as this study focuses on evaluation of contemporary hunting practices.

4.4.1 Hunter Profile

All respondents identified as Orang Melayu, persons belonging to the Malay ethnic community who are practitioners of the Islamic faith. Their ages ranged from 27 to 73 years (in the year 2019) with a mean of 42.24 years (Figure C4.1 panel A). Most respondents (80%, n=20, Figure C4.1 panel B) attended primary school, and out of them, six individuals did not complete this level. Only two respondents attended and completed secondary school, which was the highest level of education recorded in this study. All respondents were homeowners and landowners. However, the size of their houses (number of rooms ranging from 1 to 4) (Figure

C4.1 panel C) and the amount of land owned (in ha; min=0.005, max=29.51, mean=3.15) varied across respondents (Figure C4.1 panel D). Most respondents (60%, n=15) owned domestic animals (Figure C4.1 panel F); all 15 respondents owned chickens (n=3 to 60), and three of them additionally owned cows (n=3), a goat (n=1), and ducks (n=5), respectively.

Household size ranged from 3 to 8 individuals, while the number of working members within each household ranged from 1 to 4 (Figure C4.2 panel A). Every household had multiple sources of income (Figure C4.2 panel B). When asked to list three primary sources of income, most respondents mentioned income from working in oil-palm plantations, including small, individually owned (36%, n=9) and large, company-owned (44%, n=11) plantations, rubber plantations owned by them (56%, n=14) or others in their village (16%, n=4), and paddy/vegetable fields they owned (n=15). A small subset of respondents listed other sources of income (Figure C4.2 panel B). The estimated monthly household income ranged from 100,000 to 11,000,000 IDR (Indonesian rupiah), with a mean of 2,898,800 IDR (or approximately 200 USD at an exchange rate of 1 USD = 14,525.1 IDR in May 2019, as per https://www.exchange-rates.org/). It is important to note that only four respondents reported an income of seven million IDR (~482 USD) or higher, while the rest reported a monthly income between 100,000 and 3,500,000 IDR (~7 and 241 USD) (Figure C4.2 panel C).

Seventeen out of 25 respondents had fathers who were hunters. At the time of the interview, respondents had been hunting for an average of 18.4 years (min=2, max=46).

4.4.2 An overview of hunting practices

Two of the surveyed households had two active hunters, while the remaining households had one active hunter (Figure C4.2 panel A). Most respondents (56%, n=14) hunted 1-2 times a month, while fewer individuals hunted 1-2 times a week (20%, n=5) or 1-2 times every 6 months

(20%, n=5). One respondent hunted 1-2 times per year (Figure C4.3 panel A). In general, the main motivations for hunting, in decreasing order, were for consumption at home (100%, n=25), monetary gain (52%, n=13), and for sport/ hobby (32%, n=8) (Figure C4.3 panel B). However, when specifically asked about their reasons for hunting each focal species, other motivations were listed, and sport/hobby was not mentioned as a motive for killing any of them (Figure C4.4). We detail these motives in a subsequent section.

A variety of techniques were used to hunt. However, hunting with locally made (*senapan angin* in Bahasa Indonesia; Figure 4.1) and/or homemade (*senapan lantak* in Bahasa Indonesia; Figure 4.1) guns were the most preferred techniques (96%, n=24; Figure C4.3 panel C). Most respondents hunted year-round (56%, n=14), while some (32%, n=8) hunted exclusively in the dry season, and fewer (12%, n=3) hunted during the paddy harvest season or fruiting season (including both forest and village / plantation fruits) (Figure C4.3 panel E). All respondents hunted in the forest (n=25), and six of them (24%) also hunted in their plantations/farms (Figure C4.3 panel F). Most hunting sites were located within two hours from their residences (72%, n=18; Figure C4.3 panel G). Yet, 11 respondents (44%) reported that they often slept in the forest during hunting trips, while six (24%) rarely slept in the forest, and eight (32%) never slept in the forest on hunting trips.

4.4.3 Hunting of focal species

Out of the 33 focal species presented, many respondents did not recognize or were confused about the identity of species from certain groups, mostly civets, squirrels, and hornbills (Table C4.2). The following results exclude instances when species were not recognized or misidentified. Among the species definitively identified, respondents stated that at least 26 species were hunted. Out of these, 10 species were sought after or preferred, while 16 were opportunistically hunted (Figure 4.2). All respondents stated that they preferentially hunted all species of deer and mouse deer (inset figure in Figure 4.2). Another group of species that were preferentially hunted were porcupines, with 20 (80%), 18 (72%), and 9 (36%) respondents stating that they preferred Malay porcupines (inset figure in Figure 4.2), thick-spined porcupines, and long-tailed porcupines, respectively. Those who did not prefer or did not hunt long-tailed porcupines stated that, while hunting it is not prohibited by religious norms, they do not want to eat it due to its 'rat-like' appearance.

One respondent listed the large flying-fox as a preferred species for its medicinal value. Few respondents (24%, n=6) chose helmeted hornbills as a preferred species, which is exclusively hunted for its casque, which is sold at a high price (see Figure 4.3) in the domestic black market. However, we strongly believe that the harvest and trade of this species were underreported in our study, as several respondents were visibly wary when we asked questions about this species. This may also be true for at least two other species: the Bornean orangutan and Sunda pangolin (which was not among our focal species but came up in conversations). Private conversations with respondents and other villagers indicated that this wariness stemmed from the fear of legal repercussions. Even though many respondents (56%, n=14) did not know that hunting was illegal as discussed in a subsequent section, several noted that the national park office specifically prohibits the hunting of species such as the orangutan, helmeted hornbill, Sunda pangolin, and possibly others that were not among our focal species and were not mentioned during conversations.

The main motivations for hunting each focal species, in decreasing order, were for consumption at home (31.3% of records, n=183), monetary gain (19%, n=111), pest control (18.5%, n=108), use in traditional medicines (14.4%, n=84), cultural and religious purposes

(9.9%, n=58), and capture of live animals for pet-keeping (6.8%, n=40) (Figure C4.4). All preferred species (inset figure in Figure 4.2) were hunted for consumption at home, for money from the sale of meat and body parts used in traditional medicines, for cultural/religious events, and/or captured live for pet-keeping (Figure C4.4). Other species that were hunted, but not preferentially, were hunted for money from the sale of body parts used in medicines, in retaliation for crop raiding or killing poultry, or were captured live for pet-keeping (Figure C4.4).

4.4.4 Meat consumption and sale

All preferred species, excluding the large flying fox and helmeted hornbill, were primarily hunted for consumption at home (Figure C4.4). Most respondents (80%, n=20) consumed wild meat 1-2 times a month. Four respondents consumed wild meat 1-2 times every 6 months, while one respondent consumed wild meat 1-2 times per year (Figure C4.3 panel D). Wild meat was sold less frequently than it was consumed, with 11 respondents (44%) reporting never selling it and 9 respondents (36%) selling it 1-2 times a year (Figure C4.3 panel D). The primary reason for the infrequent sale of wild meat was the limited availability of animals, particularly sambar. In this context, respondents rarely had the opportunity to hunt many or large animals. When sold, earnings from the sale of one kilogram of meat from larger animals, sambar, and muntjac, ranged from 50,000 to 150,000 IDR, with a mean income of 82,350 IDR (~6 USD) (Figure 4.4). Income from the sale of smaller animals, mouse deer, and porcupines, ranged from 25,000 to 100,000 IDR per kilogram (mean=61,875 IDR or ~4 USD), or from 40,000 to 150,000 IDR per animal (mean=70,143 IDR or ~5 USD) (Figure 4.4).

A total of 13 respondents (52%) reported consuming domestic meat 1-2 times per week, while 10 (40%) of them consumed domestic meat 1-2 times per month. The remaining respondents consumed domestic meat less frequently (Figure C4.3 panel D). Among the respondents who consumed domestic meat fewer than 1-2 times a week, cost was the primary factor for most (40%, n=10), while two others stated that store-bought chickens were "not good for our health as they are fed chemicals". When asked about their preference between wild and domestic meat, 14 respondents (56%) chose wild meat, citing reasons such as its taste, naturalness, lack of chemicals, health benefits, and aroma. On the other hand, 11 respondents (44%) chose domestic meat mainly because wild meat was considered rare and difficult to obtain, whereas domestic meat was readily available when desired, among other reasons.

4.4.5 Animals used in traditional medicines

Records of medicinal use of animals in this study include both those used by the respondents and those known to them from other members within or outside their community. A total of 16 species, including the Sunda pangolin, and two species of snakes that were not among our focal animals, were used for the treatment of over 20 health conditions (Table S3). Among these, porcupines (44.1%), sun bears (24.5%), followed by large flying-foxes (6.9%), were the most frequently reported medicinal animals (Table C4.3). With respect to body parts used in traditional medicines, gallbladder (33.1%), bezoars (24.6%), sun bear skin (9.2%), and porcupine tail (9.2%) were most commonly reported. Additionally, meat (6.3%), '*selusuh*' (a part found near the fetus in pregnant mouse deer; 5.6%), liver (4.9%), beak (2.1%), quills (1.4%), fat (1.4%), teeth (1.4%), and an unspecified part from cobras (0.7%) were also reported to have medicinal value (Table C4.3).

Gallbladders from 11 mammalian species were utilized; however, gallbladders from sun bears were most frequently reported (53.2%). Gallbladders and skin from sun bears were most commonly used (62.3%) to treat internal and external injuries from accidents, especially those that involved falling (Box 1). While 28% of the respondents didn't know the method, 64%

reported that fresh or dried sun bear gallbladders were soaked in hot water, after which the water is consumed. This method was commonly used to prepare medicine from gallbladders harvested from other species (Table C4.3). Respondents mentioned that they rarely sold gallbladders due to the difficulty in procuring them. Among the five respondents who reported selling them, they earned between 400000 – 1000000 IDR (or ~ 28 to 69 USD) per sun bear gallbladder (Table C4.3; Figure 4.3). For sun bear skin (for photo see Figure 4.1), 23.1% of the respondents didn't know the preparation method, while 46.2% reported that it was dried, powdered, mixed in water, and the resulting liquid was consumed (Table C4.3).

Harvesting bezoars for medicinal use was most frequently reported in the case of the Malayan porcupine (45.7%), followed by the thick-spined porcupine (31.4%). Bezoars were less frequently harvested from the long-tailed porcupine (14.3%) and red langur (8.6%) (Table C4.3). Despite being the second most frequently reported body part with medicinal value, 64.1% of respondents did not know its specific uses, and 68.6% were unaware of the method used to prepare medicine from it (Table C4.3). Those who were aware reported that bezoars were used to treat rheumatism (10.3%), strokes (10.3%), internal injuries (10.3%), urinary retention (2.6%), and to ensure smooth/uncomplicated labor (2.6%). The common method of preparation involved boiling or soaking dried or fresh bezoars in water, which was then consumed. Due to the scarcity of bezoars, as they are not found in the gastrointestinal tracts of every animal that is harvested, they are rarely sold. When sold, bezoars from porcupines could fetch between 340000-500000 IDR/g (or ~23-34 USD) depending on the species, while those from red langurs sold at an average price of 4500000 IDR/piece (~310 USD) or 350000 IDR/g (~24 USD) (Table C4.3; Figure 4.3).

4.4.6 Animals used in cultural and religious practices

All but six respondents noted that certain animals were sought after for religious/cultural celebrations and cultural practices. Nineteen respondents (76%) mentioned that sambar meat was served during communal feasts held for cultural and religious celebrations, such as weddings, circumcisions, births, and events from the Islamic calendar. Six respondents further elaborated that since sambar meat is now “difficult to find” or “rarely available,” domestic meat is used instead. Two of them noted that sambar meat is considered “special” and is especially sought after for such celebrations. Three respondents stated that sambar meat was extensively used earlier because “it was difficult to buy beef as it takes one day on foot to reach Sandai,” the closest town to their village. Fewer respondents noted that meat from other species, such as muntjac (n=9; 36%), mouse deer (n=8; 32%), gallinaceous birds (n=3; 12%), and porcupines (n=2; 8%), was also used during such celebrations. All respondents noted that meat from any of these animals was not considered mandatory for these celebrations.

Nine respondents (36%) noted that rhinoceros hornbills were hunted by the Dayak people for their casques and feathers, which are worn as head adornments during traditional dances and other cultural events. One respondent mentioned that the skin from sun bears is used as a preventive measure against '*ilmu hitam*' black magic, while three noted that bones of slow lorises are used to perform black magic.

4.4.7 Local taboos/prohibitions

Respondents stated that beliefs passed on from earlier generations permit the hunting and (more strictly) the consumption of only a small subset of animals, which includes sambar, muntjac, mouse deer, porcupines, and gallinaceous birds (pheasants, quails, and other land fowl). These species were considered ‘*halal*’ (permissible or lawful in Islam), while all other species were considered ‘*haram*’ and therefore must not be eaten. Respondents also observed that it was acceptable to kill animals such as bearded pigs (84% of respondents), long-tailed macaques (80%), pig-tailed macaques (84%), squirrels (20%), and large flying-foxes (8%) that destroy crops, and civets (56%) that kill domestic fowl, but it is forbidden to consume their meat. Upon being killed, the carcass is more frequently (71.3% of records) discarded, or more rarely (28.7%) given away free of cost to friends from the Dayak community where such prohibitions do not exist. It is considered '*haram*' to accept money in return, especially in the case of bearded pigs.

While all respondents agreed that hunting hornbills for food was forbidden, 64% provided a specific reason pertaining to toe orientation. They noted that birds such as hornbills, which have two toes pointing forward and two pointing rearwards, have '*kibak*' or '*kibah*' and are considered '*haram*'. However, birds that have three forward-facing toes and one rearward-facing toe, like chickens, were considered '*halal*'. When we further inquired about the consequences of eating meat from any of the prohibited animals, respondents stated that eating such meat would cause skin diseases, skin allergies, itchy skin, rashes, ulcers, and abscesses, especially if they ate meat from hornbills.

Slow lorises, although not one of the focal species, were regarded as dangerous, scary, and toxic by a majority of respondents (n=22; 88%). They hold the belief that slow lorises are harbingers of bad luck, leading to various superstitions surrounding them. Consequently, catching slow lorises or bringing either live or dead ones into homes is strictly forbidden ((n=17, 68%). Moreover, their bones are considered "evil," and beliefs dictate that people should refrain from bringing them into or even dropping them in front of their homes (n=10, 40%). Failure to adhere to these beliefs is thought to invite significant financial losses, potentially leading to bankruptcy (n=10, 40%), and even causing illness for the homeowners (n=3, 12%). According to three respondents, the bones of slow lorises are used in performing '*ilmu hitam*' or black magic, intended to bring misfortune upon the recipients. When slow lorises give birth atop trees, it is believed that the trees die (n=4, 16%). Additionally, respondents shared that slow loris urine is believed to be so toxic that it can kill trees (n=19, 76%). The affected tree will appear as if it has been poisoned or struck by lightning, causing the leaves to fall off. Subsequently, the bark, trunk, and roots will also perish.

While hunting primates for food is strictly prohibited by religious beliefs, 12 (48%) of the respondents listed additional reasons for prohibiting the hunting of Bornean white-bearded gibbons by both villagers and outsiders. The respondents expressed fondness for the species as they pose no threat to crops (41.7%) and have “melodious” calls (41.7%), which serve as “natural” or “traditional” alarms. Additionally, they were described as “gentle” (8.3%) and “beautiful” (8.3%), and were locally regarded as a protected species (8.3%). However, capturing live animals for pet-keeping was not only accepted but also favored. Bornean white-bearded gibbons were the most frequently captured live animals for this purpose (37.5%, Figure S4). Although they were rarely sold as pets, when they were, their price ranged from 90,000 to 200,000 IDR per animal (n=3; mean=126,666.7; Figure 4).

4.4.8 Factors influencing the frequency of hunting

Out of the 46 ordered logit models compared, the model with the frequency of wild meat consumption as the only predictor of hunting frequency emerged as the best model, with the lowest AICc and an Akaike weight of 0.35 (Table C4.4). A model with the age of respondents and the frequency of wild meat consumption as predictors emerged as the second-best model (Akaike weight = 0.16; Table C4.4). Together, these models accounted for approximately 51% of the Akaike weight.

Plotting the predicted probabilities of each outcome from the best model showed that the probability of each category of hunting frequency mirrored each category of wild meat consumption frequency (Figure C4.5 panel A). The probabilities of hunting 1-2 times a month and 1-2 times a week were both higher for respondents who consumed wild meat 1-2 times a month (Figure C4.5 panel A). On the other hand, for respondents who consumed wild meat less frequently, the probabilities of hunting less frequently were higher. Plotting the predicted probabilities of each outcome from the second-best model showed a similar pattern to the best model regarding the probability of hunting as a function of wild meat consumption (Figure C4.5 panel C). The predicted probabilities based on the second predictor (age of respondents) in this model indicated that older respondents hunted more frequently, albeit only marginally so, than their younger counterparts (Figure C4.5 panel B). While these results are consistent with our finding that food was the main motivation for hunting, they should be interpreted with caution due to our small sample sizes and resulting large confidence intervals.

4.4.9 Threats from hunting to large animals

We modeled hunting as a function of the body weight of focal animals. The output of the generalized linear model (family=binomial) shows that the odds of hunting increased with an increase in body weight (Figure 4.5). When compared with our reference level, small animals (<1 kilogram), the odds of hunting for large animals that were 1-10, 10-50, and 100-250 kgs increased by 3.7 (±1.3 SE), 17.0 (±1.44 SE), and 44.3 (±1.78 SE) respectively (Figure 5). The odds of hunting large animals that were 50-100 kgs animals were only marginally higher, 1.22 (±1.70 SE), than our reference level. The latter category included a single species, the Bornean orangutan. As discussed in the preceding section, there are reasons to think that our data underestimate hunting frequencies of this taxon..

4.4.10 Conservation status of focal species

Based on the observed changes to populations over the last three decades, a majority of respondents noted that populations of preferred species, specifically sambar, mouse deer, muntjac, and Malayan porcupine, have undergone extreme to moderate levels of decline (Table C4.5). Among the other preferred species, a majority of respondents reported that populations of thick-spined porcupines, long-tailed porcupines, and large flying-foxes were stable. Opinions on the status of helmeted hornbills were divided, with an equal number reporting extreme decline to no decline. Hunting by both Melayu and non-Melayu people was identified as the main driver of population declines across species.

All respondents reported that sambar populations had critically declined or had been locally extirpated. The primary reason listed was overhunting by both Melayu and non-Melayu people (100% of respondents), followed by deforestation from the expansion of oil-palm plantations (5%) and a slow reproductive rate (4%). Apart from five independent, recent records of sambar from five respondents, including one currently caged individual (Figure 4.1), two individuals hunted within the last year, and two more hunted around 4-6 years ago, all other respondents stated that they hadn't seen a sambar in a very long time.

Sixty percent of respondents stated that the Bornean orangutan population had critically declined, which they attributed to deforestation (73.3%), overhunting by Dayak people (66.6%), and a slow reproductive rate (20%). Furthermore, 56% of respondents noted that populations of both species of mouse deer had critically declined due to overhunting by both Melayu and non-Melayu people (100%) and deforestation (21.4%). With respect to populations of the red and Bornean yellow muntjac, 40% and 36% of respondents, respectively, reported critical declines, while 32% reported moderate levels of decline for both species, primarily attributing it to overhunting by both Melayu and non-Melayu people (100%), with only two respondents each additionally noting deforestation as a cause.

In the case of porcupines, which were hunted for food and medicinal use, 56% of respondents stated that Malayan porcupine populations had moderately declined, while 60% and 24% maintained that populations of long-tailed porcupine and thick-spined porcupine were stable or had undergone no change. Regarding sun bears, which were exclusively hunted for medicinal use, 36% reported critical declines, 20% reported moderate declines, and 36% reported stable populations. As for helmeted hornbills, hunted for their valuable casques, 28% and 20% reported critical declines and moderate declines, respectively, with 28% reporting no decline. Finally, large flying-foxes, preferentially hunted by a few respondents for their medicinal value, reportedly experienced no change in their population, according to 72% of respondents.

4.4.11 Perceptions towards hunting

All but one respondent noted that hunting was becoming increasingly difficult. Nineteen of them (79%) attributed this to low animal abundance, while the rest listed other reasons, including age and/or their own deteriorating health (29%), greater travel times to hunting sites (16.7%), decrease in forest cover (12.5%), prohibitions by the national park office (4%), and difficulty in locating animals within the national park given its size (4%). The sole respondent who stated that hunting was not difficult said, “I still have the energy, and even at times when I am feeling unmotivated and receive information about the presence of sambar, I have the drive to go hunting.”

Seventy-two percent of respondents (n=18) noted that they were worried that wild animals are now rarer. The reasons for this concern ranged from not being able to eat wild ‘halal’ meat (n=7), loss of income from the sale of meat or other animal parts (n=3), “my children and grandchildren can no longer see animals like the sambar” (n=2), “mu children and grandchildren will not be able to eat wild meat” (n=1), “animals like sun bears, known as the 'kings of the forest,' are no longer there to take care of the forest, and when they become rare, it will be difficult to get gallbladders” (n=1), “now there are no animals; earlier, animals like gibbons would sing and their songs served as a morning alarm, given that clocks were not available” (n=1), loss of seed dispersers for plants like Durian (n=1), to “the forest is not nice when it is empty” (n=1), “I still have a desire to hunt” (n=1) among other reasons.

Sixteen respondents (64%) stated that they were aware that hunting wild animals was illegal, while all respondents perceived hunting as a risky activity. Risks according to them included accidentally shooting someone, being shot by someone, or other accidents (68%; n=17), being attacked by wild animals (32%; n=8), getting caught by national park guards for hunting and carrying guns (28%; n=7), and losing their way in the forest (16%; n=4), among others.

Most (88%, n=22) respondents stated that they did not wish to continue hunting because they are getting old, are no longer capable, and/or do not have the energy to hunt (64%, n=16). Other reasons included low animal abundance (32%, n=8), high risks (20%, n=5), and low returns given the effort put in (8%, n=2). Three of the respondents stated that they would continue hunting depending on the availability of certain animals like sambar. One respondent stated, “Even if it is prohibited, I cannot stop as it is in my blood.” Most respondents (92%, n=23) noted that they would dissuade their children from hunting because it would be better for them to avoid the risks associated with hunting (44%, n=11), focus on education (36%, n=9), and pursue better (and more lucrative) opportunities to have a better life (36%, n=9), among other reasons.

4.4.12 Overview of hunting practices by former hunters

The four former hunters (mean age=74.8 years; SD=3.3) we interviewed noted that they had hunted for an average of 18-20 years (mean=19.5) before stopping around 1997 (n=1) and 2000 (n=3). They attributed this to the risks of hunting in the national park (n=3), age-related limitations (n=3), investment of more time in working in rubber plantations to boost income (n=1), and the declining sambar populations (n=1). Initially, their primary occupations were logging ironwood *Eusideroxylon zwageri* (n=3), collecting non-timber forest products (n=3), and working in rubber plantations (n=4). Subsequently, around the year 2000, they worked full-time in rubber (n=4), and recently established oil-palm (n=3) plantations.

When they used to hunt, all respondents hunted at least once a week and sometimes more frequently. They mostly hunted within their rubber plantations and paddy fields, with only one respondent occasionally hunting in the forest. These hunting locations were close, typically within an hour's walking distance. The respondents employed various hunting methods, including using dogs and spears (n=1), traps and spears (n=1), spears and machetes (n=1), traps (n=1), and homemade guns (n=2).

They noted that their fields and plantations, which were then surrounded by forest, attracted a variety of wild animals, including sambar, pigs, and macaques. These animals, including the sambar, often caused damage to their crops, leading to their culling for pest control. Interestingly, they noted that the name '*Rusa*' stems from the Bahasa Indonesia word '*merusak*,' which means damage or destroy. While pig and macaque carcasses were discarded, the meat of the sambar was harvested for consumption. The sambar, the most commonly hunted animal, was targeted by many hunters frequently. It was their preferred source of meat, often consumed during religious and cultural celebrations. Apart from sambar, they also hunted muntjac, mouse deer, and Malayan and thick-spined porcupine, but the long-tailed porcupine was never hunted. The harvested meat was mainly consumed at home, shared with neighbors, or bartered for essentials like rice or an ironwood plank; it was never sold.

Wild meat was an essential component of their diet, consumed at least once a week and sometimes more frequently. In contrast, domestic meat was a rarity, being consumed only 1-3 times a year due to its scarcity. Additionally, various animal parts such as sun bear gall bladders (used for internal injuries; n=4), sun bear skin (used during illnesses; n=2), sambar antlers (used for joint pain; n=2), Malayan porcupine bezoars (used to aid in smooth labor; n=2), and large flying-fox liver (used to treat cough and lung disease; n=3) were utilized for medicinal purposes.

Their religious beliefs dictated that they could only consume specific animals, like deer, mouse deer, porcupines, and gallinaceous birds. Cultural taboos prevented them from catching or bringing slow lorises, whether alive or dead, or their bones home, and not adhering to these beliefs was believed to bring bad luck and heavy financial losses. Additionally, their urine was considered toxic enough to kill trees.

Respondents noted that the main difference between their hunting experiences then and the present is the decreased abundance of animals and, therefore, the infrequency of hunting and eating wild meat, particularly the sambar, and the decline in forested areas.

4.5 Discussion

Melayu hunters were extremely selective in the animal species they targeted, mainly due to religious prohibitions as reported by former and currently active hunters. Our results indicate that select prey species, specifically deer and mouse deer, were highly sought after for their meat by all respondents, and they faced the greatest threat from hunting, potentially being overharvested. This is a common occurrence across SE Asia, where ungulates are disproportionately targeted and overharvested to meet local and regional demands for meat and other body parts. Consequently, this has led to declines in population sizes across their range and site-level extirpations (Ali et al., 2021; Corlette, 2007; Goldthorpe and Neo, 2011; Luskin et al., 2014; Sodhi et al., 2004; Steinmetz et al., 2010).

While populations of ungulate species like pigs and muntjacs have shown resilience to hunting or the capacity to recover when hunting stops, it has been observed that populations of sensitive species like sambar when overharvested fail to recover even after hunting ceases (Steinmetz et al., 2010). In our study, all respondents reported critically low populations or the absence of sambar due to overhunting when compared to other targeted species. Although no animal of significant cultural importance was reported by respondents in our study, the sambar held a special place, with early hunting exclusively targeting it, and its meat still being highly favored for consumption at home, and especially during cultural and religious celebrations. As a result, the absence of sambar from the landscape may be more profoundly experienced compared to other species. Apart from ungulates, porcupines, particularly the Malayan porcupine, heavily exploited for meat and other body parts, and widely traded across Asian markets (Brooks et al., 2010; Gomez et al., 2021; Heinrich et al., 2020), were the only other group that was preferentially targeted for food by most respondents.

Overall, our results indicate a preference for hunting large animals, as the odds of hunting increased with body size. This finding is consistent with the broad pattern observed pantropically (Benitez-Lopez et al., 2019; Harrison et al., 2016; Ingram et al., 2021; Ripple et al., 2016) and regionally, from indigenous communities in West Kalimantan (Wadley et al., 1997), Papua (Pangau-Adam et al., 2012), and Sarawak (Yi and Mohd-Azlan, 2020), to several ethnic communities with distinct hunting practices in the Jambi province of Sumatra (Luskin et al., 2014). All show a preference for hunting large animals, particularly ungulates. A rare exception was found among indigenous communities from Peninsular Malaysia, who preferentially hunted medium-sized arboreal mammals that were easier to kill with traditional blowpipes, their preferred hunting tool (Loke et al., 2020).

While in the past, hunting with spears, dogs, traps, and homemade guns was favored, the hunters we interviewed who are currently or have been recently active predominantly used modern hunting methods. They show a clear preference for locally available and homemade guns over more traditional methods. A preference for guns has been observed earlier on in Borneo (Bennett et al., 2000; Wadley et al., 1997), and still remains the preferred method at some sites (Kurtz et al., 2021). The use of traditional methods like bows and arrows in Papua (Pagau-Adam et al., 2012), or blowpipes by the Jahai community in peninsular Malaysia (Loke et al., 2020) seems restricted to remote sites. Snares, unlike guns, are less detectable and require less time investment, and for these reasons, they are widely used by hunters across SE Asia (Figel et al., 2021; Gray et al., 2018). Surprisingly, the use of snares was infrequently reported by respondents in our study.

Our results indicate that hunting frequency was primarily driven by the frequency of wild meat consumption. However, a majority of participants hunted and consumed wild meat infrequently, mostly 1-2 times a month or even less frequently. In contrast, former hunters used to eat wild meat at least once a week, if not more frequently. This suggests that wild meat is no longer a critical component in the diets of these rural communities. Two previous studies have identified a consistent trend. Bennett et al. (2000) reported that only 4.1% of meals consumed by immigrant plantation workers consisted of wild meat, while Luskin et al. (2014) found that only

3.9% of meals consumed by various ethnic communities living in a plantation landscape included wild meat. While Bennett et al. (2000) attributed the infrequency of eating wild meat to the lack of time and means in the case of immigrant plantation workers, our results suggest a different perspective. We found that the low consumption of wild meat, despite a preference for it, was associated with the scarcity of preferred species like sambar and the easier availability of domestic meat. This is evidenced by the increased frequency in consumption of domestic meat when compared to wild meat by former hunters. Luskin et al. (2014) also posited that the widespread availability of affordable domestic meat could have contributed to the decreased reliance on wild meat.

Hunting for trade was even rarer, as harvests were rarely large enough to be sold; instead, they were just sufficient to be consumed at homes. This was attributed to low animal populations, which resulted in fewer opportunities available to harvest many animals or large animals like sambar. This is a considerable departure from the reason for no trade given by former hunters, who noted that sambar was abundant, never sold, only shared, or bartered. On rare occasions when active hunters sold meat, highly preferred sambar meat fetched an average price of 6 USD/kg, only marginally higher than the average prices reported from Papua (1-3 USD/kg, Pangau-Adam et al., 2022; Pattiselanno and Nasi, 2015;), Sarawak (estimated at 5 USD/kg, assuming the weight of sambar to be 200kg; Yi and Mohd-Azlan, 2020), and Sabah (2 USD/kg; Wong et al., 2012). Although other opportunities for monetary gain from the sale of wild meat were available, respondents could not benefit from them due to religious reasons. Meat from generalist species, like pigs, known to thrive in mixed-use landscapes (Luskin et al., 2014), is highly sought after by non-Muslim communities, and the trade in wild pigs serves as an important source of income for many rural communities across SE Asia (Luskin et al., 2014;

Milner-Gulland and Clayton, 2002; Pangau-Adam et al., 2012; Wong et al., 2012; Yi & Mohd-Azlan, 2020). While most respondents reported that pigs were regularly culled for pest control, aligning with observations in other plantation-dominated landscapes in Malaysia and Indonesia (Jambari et al., 2012; Kurtz et al., 2012; Luskin et al., 2014), their carcasses were more often discarded or freely given to individuals from neighboring Dayak Christian communities. They attributed this practice to age-old religious prohibitions against selling meat from ‘*haram*’ animals. This differs from Luskin et al.’s (2014) observations of hunting habits among Muslim groups in Sumatra, where consumption of wild pig meat was similarly prohibited, but the hunting and selling of wild pigs were not banned. In general, our results indicate that despite improved connectivity to markets and the availability of opportunities to sell wild meat and other animal parts from animals whose populations were perceived to be stable, hunting was not practiced for economic gain and was not a main source of income for any of our respondents. However, monetary gain from certain species, such as the helmeted hornbill, could be underreported due to the fear of legal repercussions. Recent records of seizures and ground reports reveal a significant increase in trade and demand for the casque of the Critically Endangered Helmeted Hornbill from the forests of Indonesian Borneo and Sumatra (Beastall, 2016; Collar, 2015; Jain et al., 2018). Ten of our respondents reported the local sale value to be ~218 USD/g, although sales were reported as rare. To put this in perspective, the average monthly household income reported in our study was ~191.88 USD. However, as noted earlier, there was visible wariness when we asked questions about this species, and this may be attributed to the fact that trade is strictly regulated, with heavy penalties imposed on poachers when caught (Beastall, 2016). We are not certain about the hunting pressures experienced by this species based on data from this study.

While religious norms forbade eating and selling (particularly in the case of pigs) meat from ‘*haram*’ animals, which included all other species barring deer, mouse deer, porcupines, and gallinaceous birds, harvesting them for medicinal use was not prohibited. The medicinal use of bezoars more commonly obtained from Malayan porcupines than thick-spined porcupines, and gall bladders from sun bears, a ‘*haram*’ animal, accounted for a majority of records. Ethnozoological studies across Indonesia, note that the Malayan porcupine was the most frequently referenced medicinal animal, with the sun bear also mentioned among the top medicinal animals (Mardiastuti et al., 2021).

The trade in porcupine bezoars has a rich historical presence spanning centuries and continues to expand, encompassing both physical markets and the burgeoning e-commerce sector (Heinrich et al., 2020). Sites in Borneo, particularly Kalimantan, are now emerging as potential trade hotspots, primarily due to the high value associated with bezoars from Bornean rainforest porcupines (Tan et al., 2019; Heinrich et al., 2020; Gomez, 2021). This emergence may be attributed to stricter control of porcupine bezoar sales in neighboring Malaysia (Tan et al., 2019).

In our study, few respondents were aware of the utility value of bezoars and reported selling them, albeit infrequently. This was because bezoars were rarely obtained since only a small proportion of harvested animals had them. This observation aligns with findings noted by Tan et al., (2019) and Heinrich et al., (2020). When sold, they were offered at substantially lower prices, more comparable to what Gomez et al., (2021) reported from West Sumatra (~11 USD/bezoar) than when traded commercially. Studies that assessed commercial trade have reported the average price per gram to be 119.3 USD, 182.8 USD, and between 73-650 USD

(Heinrich et al., 2020), which is close to twice the current price of gold per gram. Respondents in our study reported selling a gram at an average price of 25.5 USD (n=4).

The utility value reported by the few respondents who knew about it was found to be markedly different from what other studies report regarding the use of bezoars. In those studies, bezoars are primarily used in Traditional Chinese Medicines (TCM) to treat cancer, diabetes, dengue, typhoid, epilepsy, hepatitis, and other serious ailments (Tan et al., 2019; Heinrich et al., 2020).

On the contrary, the majority of respondents demonstrated awareness regarding the use of gallbladders, which were predominantly harvested from sun bears, for medicinal purposes. Due to their significance in traditional medicine and their limited availability, gallbladders were mostly retained for household use by respondents and seldom sold, with an average price of 44 USD per piece based on a small sample of 5 transactions. The information presented in the study closely corroborates with previous reports from Malaysian Borneo (Yi and Mohd-Azlan, 2020). Despite variations in ethnicity, the methods employed for preparing derivatives from gallbladders were found to be similar. And, illegally sold gallbladders fetched a comparable price of 36 USD per piece, highlighting similarities in use and trade (Yi and Mohd-Azlan, 2020). An earlier study from Kalimantan (Meijaard, 1999) suggested that the average price of a single gallbladder was 33 USD. Despite the growing commercial demand for sun bear derivatives from the wild, with Indonesia often featuring as a key supplier (Gomez and Shepherd, 2019; Gomez et al., 2019), local prices of gallbladders may not have significantly deviated and might still be comparable to what it was two decades ago. Meijaard (1999) noted that the low availability of bear gallbladders in shops, combined with low prices in Kalimantan, suggested a low demand. However, more recent studies suggest a different scenario now, reporting widespread trade of bear parts and derivatives, including gallbladders, based on seizures, with many of them reportedly sourced from Kalimantan (Gomez et al., 2019), raising concerns about the sustainability of such trade and its potential impact on sun bear populations in the region.

While most prohibitions with respect to hunting and use of wild animals were rooted in religious beliefs, cultural taboos were reported exclusively in the case of slow lorises. Despite being heavily exploited to feed the ongoing and rampant illegal pet trade across their range (Nekaris and Starr, 2014; Nijman et al., 2017), slow lorises were strictly avoided by all respondents due to various superstitions surrounding the species. Remarkably, the beliefs described here were identical to those held by certain Sundanese communities from Southern Java, known for their strong traditions, taboos, and deeply rooted beliefs (Nijman and Nekaris, 2014). It was observed that cultural taboos may act as a safeguard, deterring local communities from participating in the illegal trade, and can thus aid in the protection of otherwise highly threatened species like the slow loris (Nijman and Nekaris, 2014). However, to what extent these beliefs are upheld at our specific site or extend beyond it remains unclear. Ongoing monitoring efforts of slow loris trade by organizations such as the International Animal Rescue routinely report the seizures of illegally captured animals in West Kalimantan, indicating that trade and capture of slow lorises persist in the region (International Animal Rescue, 2015).

Finally, our results highlight a declining interest by individual hunters in pursuing hunting, largely due to dwindling populations of preferred species and risks associated with age-related physical limitations. Interestingly, legal risks of hunting within protected areas were not considered a significant deterrent, and many respondents admitted to being unaware of relevant laws, regulations, and the protection status awarded to wildlife under Indonesian laws. However, a small number expressed enthusiasm and willingness to continue hunting, contingent on the availability of specific species like sambar.

4.6 Conclusion

Overall, our study reports that Melayu Muslim communities were highly selective in the species they targeted for hunting, especially for food, the main motivation for hunting. We observed that wild meat was no longer a critical component of their diet and not an important income source. However, we further noted that populations of ungulates, particularly sambar, might be critically declining due to overharvesting. The depletion of large ungulates from tropical forests stands to affect fundamental ecological processes, including the dispersal of large seeds (Brodie et al., 2009a,b; Prasad et al., 2006) among others. However, the downstream impacts are difficult to predict given our current limited understanding of seed dispersal services provided and herbivory by large ungulates to plants in Asian tropical forests (Sridhara et al., 2016).

Our study comes with several notable limitations. Firstly, we must acknowledge that we did not investigate the actual impact of hunting on prey densities. Thus, there is a possibility of bias regarding the conservation status of wildlife, reported solely based on perceptions. We also acknowledge other potential sources of bias stemming from a) non-truthful disclosures by survey participants, especially concerning the hunting of commercially traded species, and b) errors associated with recall data. However, despite the limitation of a small sample size, we are confident that our study has successfully captured the dominant trends of hunting practices among Muslim Melayu communities in this mixed-use landscape. This confidence is based on our understanding that strictly observed religious norms across Muslim Melayu communities in this landscape are unlikely to change the major trends captured by our study, even with increased participation. Lastly, moving forward, we recommend conducting assessments of densities of heavily targeted prey species, specifically the sambar. Moreover, we advocate for increased efforts by the national park management to work with local communities in creating awareness about wildlife laws and regulations.

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4.9 Figures

Figure 4.1. Clockwise from the top-left corner, a) A Google Earth image illustrating the mixed-use landscape at the northeastern boundary of Gunung Palung National Park (Google Earth 2017), b) a juvenile southern pig-tailed macaque, c) captive greater oriental mouse deer, d) sun bear skin, e) a homemade gun (*Senapan lantak*), f) a locally purchased gun (*Senapan angin*), g) captive Malayan porcupines, and h) a young captive sambar.

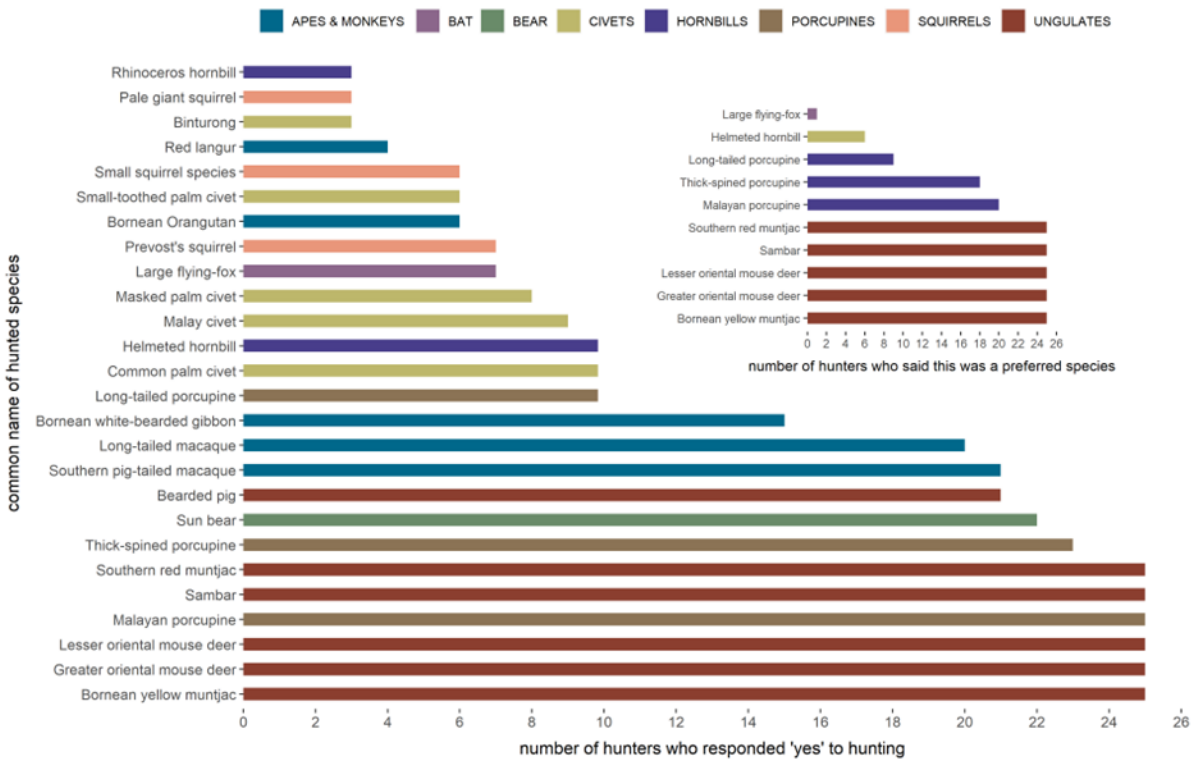

Figure 4.2. Count of hunters who responded affirmatively to hunting 26 focal animal species. The inset figure offers a breakdown of the number of hunters who designated ten focal animal species as preferred. Preferred animals are described as those actively sought by hunters, as opposed to animals encountered opportunistically.

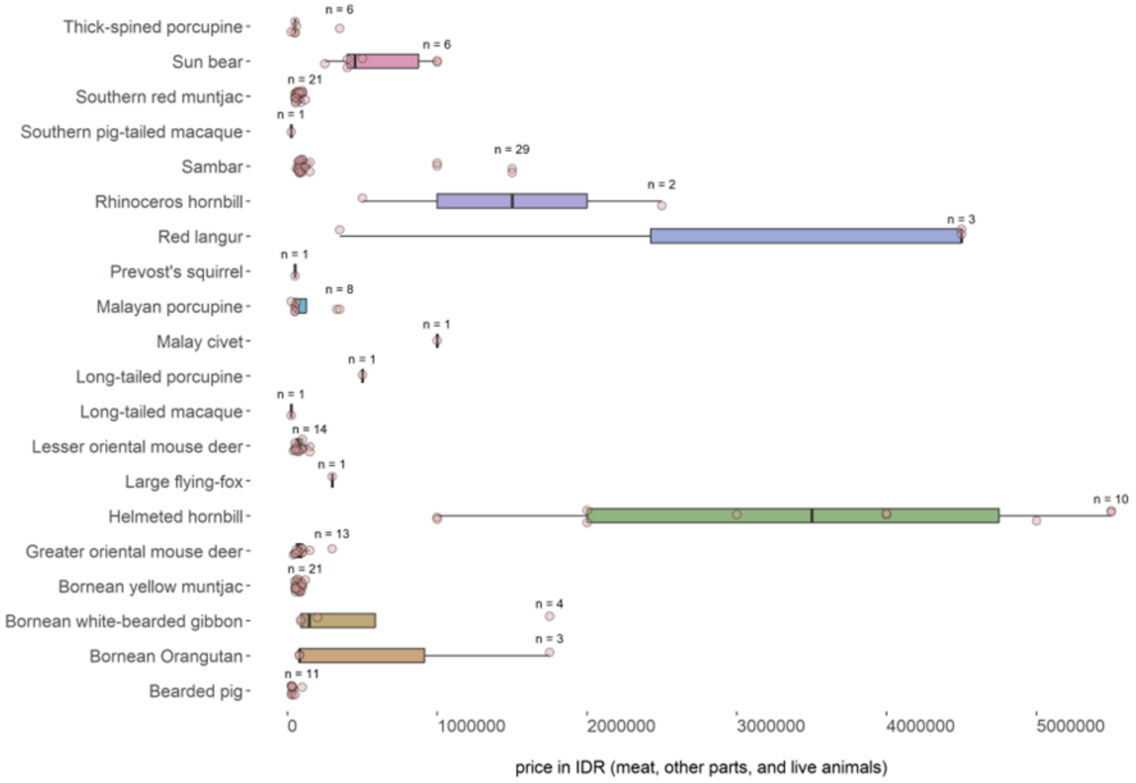

Figure 4.3. Box and whisker plots illustraing the sale price, in Indonesian rupiah (1 USD = 14525.1 IDR in May 2019), of wild meat per kilogram or the entire animal, other body parts, and per live animal for different focal animal species. The sample sizes of hunters who provided this information are displayed next to the respective box and whisker plots.

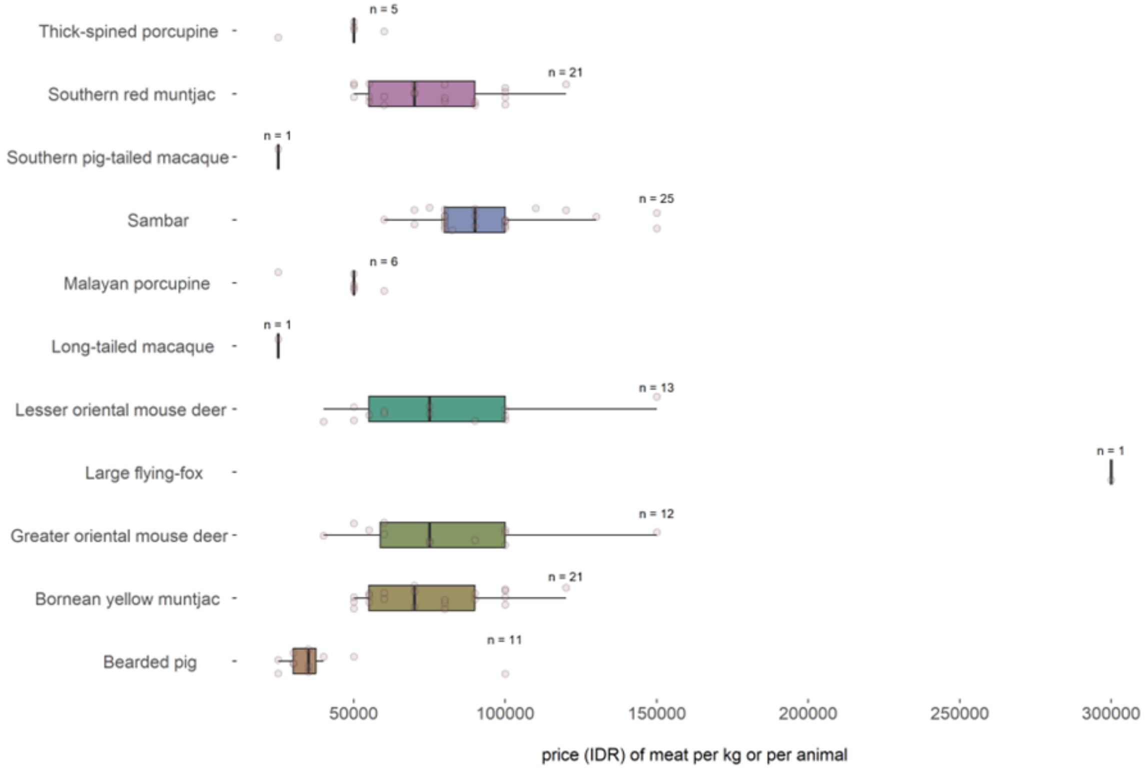

Figure 4.4. Box and whisker plots illustrating the sale price, in Indonesian rupiah (1 USD = 14525.1 IDR in May 2019), of wild meat per kilogram or the entire animal for different focal animal species. The sample sizes of hunters who provided this information are displayed next to the respective box and whisker plots.

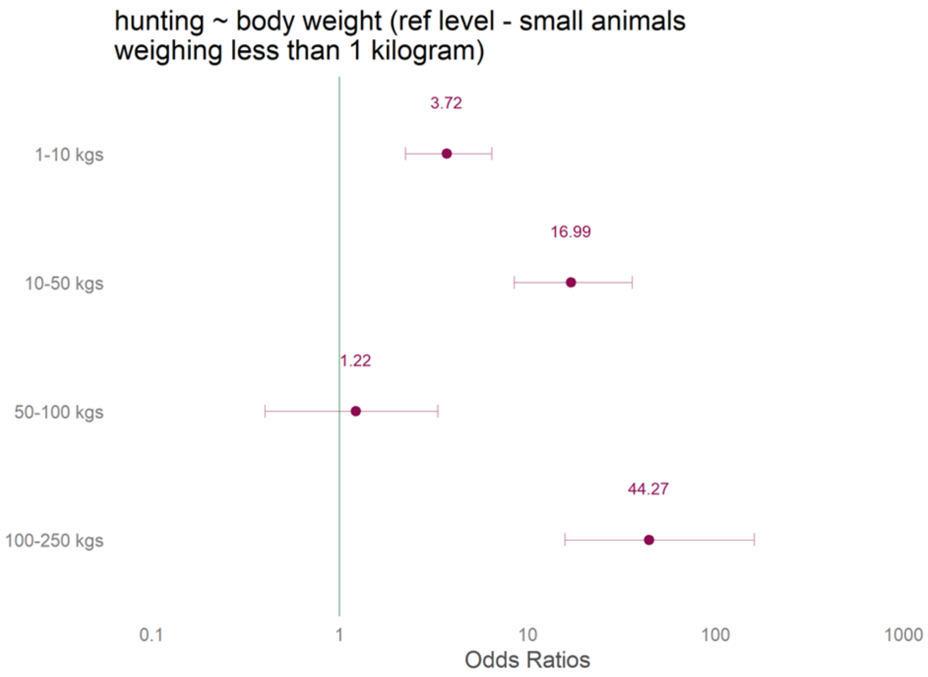

Figure 4.5. Odds of being hunted, a binary variable, relative to animal body weight categories. Body weight data of the 33 fruit-and seed-eating mammal and large bird species body weight (kg) is denoted as midpoints for weight ranges and gender variations. The coefficient plot illustrates model estimates for the impact of body size on hunting odds, with the exact values displayed above each bar post-log scale transformation. Points denote coefficient estimates, while error bars signify 95% confidence intervals. The green line at one indicates no effect, and rightward points indicate higher hunting odds. Estimates with error bars that do not overlap the no effect line are reliable estimates.

Chapter 5: Conclusion

5.1 Synthesis

Fruit-frugivore interactions in tropical forests, whether mutualistic or antagonistic, profoundly impact plant reproductive success (Bello et al., 2021; Browne et al., 2018; Howe and Smallwood, 1982; Nathan, 2006). Unfortunately, these frugivores often become prime targets for hunters (Harrison et al., 2016; Ripple et al., 2016), leading to profound impacts on forest diversity, structure, and function (Caughlin, 2015; Chanthorn et al., 2019; Terborgh, 2013). While comprehending the ecological consequences of defaunation is crucial, community-level studies addressing region-specific patterns and assessing the repercussions of frugivore loss on ecosystems are largely lacking in many tropical regions (Albert-Daviaud et al., 2022). Biodiverse Southeast Asian forests continue to grapple with formidable challenges arising from human-induced land-use changes and declining wildlife populations, especially among large-bodied species (Harrison et al., 2016). Consequently, opportunities to investigate vital relationships between plants and frugivores in diverse assemblages are rapidly diminishing, and it is therefore imperative to study community-level assessments in the few remaining areas that still harbor relatively high plant diversity and populations of large-bodied frugivores.

Chapter 2: Large-Bodied Frugivores: Critical Mutualists within Fruit-Frugivore Interaction Networks of Large-Seeded Plant Species in a Bornean Lowland Rainforest.

Investigating fruit-frugivore networks in diverse tropical ecosystems is complex yet imperative (Simmons et al., 2018), especially given the widespread depletion of large-bodied animals, including frugivores (McConkey et al., 2015; McConkey et al., 2018; Ripple et al, 2016), and the potential loss of irreplaceable mutualistic interactions. In this chapter, I characterized a fruit-frugivore network encompassing 19 species of large-seeded lianas and trees and 25 animal species that interacted with these plants. My investigation entailed assessing the magnitude and direction of interactions between fruit and/or seed-eating animals and large-seeded plants. Furthermore, I scrutinized the influence of plant and animal functional traits on the likelihood of positive-neutral interactions. My findings reveal a modular yet less nested (compared to networks in other SE Asia forests) frugivore-plant interaction network, showcasing a moderate level of specialization. This network is marked by specialization among certain frugivores, generality among many, and relatively low overall connectivity, with interactions distributed unevenly among species. Moreover, the results illustrate the influence of seed weight and animal weight on the likelihood of positive-neutral interactions, underscoring the prevalence of antagonistic interactions compared to mutualistic ones.

Chapter 3: To eat or to move: Investigating mutualistic and non-mutualistic interactions within a seed predator network in Indonesian Borneo's lowland rainforests.

Seed predators' interactions with dispersed seeds are influenced by factors such as resource availability, seed traits, and biology (Lichti et al., 2017). These interactions yield variable effects on seed survival, establishment, and plant diversity (Terborgh, 2012; Wang and Smith, 2002). Assessing multispecies interactions is crucial to understand their collective impact on plant reproductive success. In this chapter, I evaluated the post-dispersal seed fate of 15 large-seeded lianas and trees, revealing a diverse range of seed predators and secondary dispersers. Predation rates decreased with distance from parent plants, and higher-density clusters beneath the canopy experienced reduced predation. Vertebrate seed predators, encompassing both large and small sized generalists, emerged as the primary agents affecting seed mortality, with varying responses to seed size and coat robustness across species.

Chapter 4: Contemporary hunting practices in a forest-plantation mosaic landscape in West Kalimantan, Borneo, Indonesia.

Large-bodied animals, including frugivores, are disproportionately targeted by hunters across the tropics (Benitez-Lopez et al., 2019), and their loss will likely affect key ecosystem functions (Caughlin et al., 2015; Harrison et al., 2013). Yet, comprehensive assessments of hunting are lacking, especially from Indonesia, which has a thriving illegal wildlife trade market (Krishnasamy and Zavagli, 2020). In this chapter, I carried out the first multispecies assessment of hunting threats posed to 33 mammal and bird species that feed on fruits and seeds, as well as contemporary hunting practices through key informant interviews. Our results indicate a preference for hunting larger animals over smaller ones. Only a select few species, such as deer, mouse deer, porcupines, and gallinaceous birds, were consumed, while non-preferred species were culled for pest control and occasionally for medicinal use or selling animal parts, among other reasons. Overall, hunters noted a significant decline in animal populations, particularly affecting ungulates like the sambar, the largest species in the area.

5.2 Implications

In our study, we found that large-seeded plants were more susceptible to antagonistic interactions than mutualistic ones. Large-bodied animals were responsible for higher proportions of mutualistic interactions. While small seed-hoarding animals play a crucial role in providing secondary dispersal services to plants with limited dispersal agents, the potential to move seeds longer distances away from parent plants is likely greater among large-bodied mammals given their wider ranging habits. Notably, several species responsible for a higher proportion of these limited positive interactions, such as muntjacs, white-bearded gibbons, and sun bears, are currently classified as threatened (IUCN, 2022). Additionally, our study revealed that muntjacs were preferred targets for hunting, sun bears were frequently exploited for medicinal purposes, and gibbons were highly sought after as pets. This discovery has significant conservation implications, particularly in Southeast Asian forests facing biodiversity loss, especially among large-bodied taxa (Harrison et al., 2016).

The loss of these critical mutualists, without compensatory mechanisms, can be detrimental to plants (McConkey et al., 2021; Qie et al., 2019). Importantly, the loss of long-distance seed dispersal can be detrimental to plants as it is essential for maintaining gene flow, genetic diversity (Browne et al., 2018; Pérez-Méndez et al., 2016), and enabling colonization of new sites and range expansions, especially in the context of climate change (Fricke et al., 2022; Mokany et al., 2014).

Overall, the loss of animals providing mutualistic services can have profound implications for forest structure. Research has firmly linked the decline of specific taxonomic groups that offer unique dispersal services, such as primates and ungulates, to reduced forest regeneration (Gardner et al., 2019; Peres et al., 2016). Furthermore, short-term assessments of defaunated sites consistently reveal lower plant species richness, reduced densities of animal-dispersed plants, and increased densities of abiotically and non-game-dispersed plants at hunted sites (Brodie et al., 2009; Kurten et al., 2015; Nunez-Iturri and Howe, 2007; Terborgh, 2013;

Vanthomme, 2011; Wright et al., 2007). Long-term studies, although less common, provide valuable insights into the profound changes in forest structure resulting from the loss of frugivores. These studies highlight increased clustering around parent plants, impacting survival across multiple life stages due to density-dependent mortality factors, relative declines in the recruitment of animal-dispersed seeds, and consistent albeit small reductions in local tree diversity over time (Caughlin et al., 2015; Harrison et al., 2013).

However, the consequences of declines in critical animal mutualists on forest structure in Asian tropical forests remain uncertain. In the short term, declines in dispersers have led to simultaneous reductions in seed dispersal and seedling establishment, as observed in deer-dispersed species (Brodie et al., 2009a,b). Predicting long-term impacts is challenging, primarily due to the absence of comprehensive community-wide assessments of plant-frugivore interactions (Albert-Daviaud et al., 2022; Ong et al., 2021a,b), limited understanding of the seed dispersal services (among others) provided by groups such as ungulates to plants (Sridhara et al., 2016), and the coexistence of numerous species within the interaction space (Albert-Daviaud et al., 2022; Ong et al., 2021a,b).

Therefore, comprehensive community-wide assessments and monitoring the status of frugivores in response to anthropogenic pressures are essential steps to better understand and address the potential long-term consequences of declining animal mutualists on the structure and functioning of Asian tropical forests. This holistic approach will help inform conservation strategies aimed at safeguarding these vital ecosystems and the multitude of species that rely on them.

5.3 References

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Appendices

Appendix A: Supplementary, Tables, and Figures for Chapter 2

Table A2.1. List of plant species studied. GSP represents the plant species, while PT indicates the plant type, with 'T' denoting trees and 'L' representing lianas. The table includes data on fruit and seed traits as follows- FRW (average fruit weight in grams), FRL (average fruit length in mm), and FSW (average fruit skin width in mm), PUW (average pulp weight in grams), TSW (average total seed weight in grams), RAT (average ratio of pulp weight to total seed weight in grams), SNO (average number of seeds), SEW (average weight of a single seed in grams), SEL (average length of a single seed in mm), FRS (fruit shape), FRP (fruit protection), and SEP (seed protection), categorizing seed protection as 'soft' (can be broken by fingernail), 'hard' (cannot be broken by fingernail), or 'stone' (protected by a true stone).

GSP	PT	FRW	FRL	FSW	PUW	TSW	RAT	SNO	SEW	SEL	FRS	FRP	SEP
Dracontomelon costatum	T	18.0	33.3	0.0	7.7	3.1	2.6	1.0	3.1	18.6	globose	soft skin	stone
Willughbeia sp. 1	L	606.7	122.7	11.5	86.1	169.0	0.6	25.4	8.4	36.4	ovoid	thick skin or rind	soft
Willughbeia sp. 2	L	147.2	77.0	8.4	36.8	27.1	1.5	17.9	2.5	22.9	ovoid	thick skin or rind	soft
Willughbeia sp. 3	L	64.9	47.3	6.2	12.2	12.1	1.1	7.2	1.8	20.1	globose	thick skin or rind	soft
Willughbeia sp. 4	L	129.5	58.3	11.8	22.3	17.8	1.4	4.2	5.4	29.0	globose	thick skin or rind	soft
Canarium sp. 1	T	44.4	55.0	0.6	31.6	6.3	5.0	1.0	6.1	41.3	ellipsoid	hard fruit wall	stone
Canarium sp. 2	T	32.1	65.9	0.8	15.9	11.2	1.4	1.0	11.9	63.3	ellipsoid	soft skin	stone
Diospyros sp.	T	43.4	41.9	2.3	5.4	10.9	0.5	6.3	2.0	25.7	ovoid	thick skin or rind	hard
Hydnocarpus sp.	T	NA	NA	NA	NA	NA	NA	NA	NA	NA	globose	thick skin or rind	soft
Irvingia malayana	T	49.2	51.3	0.0	26.0	14.3	1.8	1.0	14.2	39.2	ovoid	soft skin	hard
Strychnos sp. 1	L	107.3	55.9	4.1	30.8	13.9	2.2	30	0.5	16.2	globose	hard fruit wall	hard
Strychnos sp. 2	L	107.9	57.0	2.9	54.9	10.8	6.1	10.2	1.1	20.5	globose	hard fruit wall	hard

Lansium domesticum	T	22.2	37.0	4.2	7.7	2.9	2.9	1.7	2.1	19.5	ovoid	thick skin or rind	soft
Parartocarpus sp. 1	T	138.1	64.3	16.7	5.3	10.4	0.6	4.8	2.2	19.1	globose	hard fruit wall	hard
Xanthophyllum sp. 1	T	13.4	30.2	2.6	4.0	1.7	2.6	1.9	1.3	14.6	globose	hard fruit wall	hard
Xanthophyllum sp. 2	T	77.4	54.0	19.0	1.5	1.7	0.9	1.5	1.2	11.8	globose	hard fruit wall	hard
Xanthophyllum sp. 3	T	62.9	49.5	16.8	2.3	1.7	1.6	1.7	1.0	11.8	ovoid	hard fruit wall	soft
Madhuca sp.	T	7.4	33.3	0.0	5.0	2.4	2.2	1.1	2.2	27.1	ellipsoid	soft skin	soft
Palaquium sp.	T	10.6	34.1	0.0	8.4	3.0	3.4	1.0	2.1	28.8	ellipsoid	soft skin	hard

Table A2.2. Comparison of Linear Mixed Models used to evaluate the influence of fruit and seed traits, and animal body weight on the odds of positive and neutral interactions (combined). The table includes key model comparison metrics such as log-likelihood (logLik), corrected Akaike Information Criterion (AICc), delta (the difference in AICc between the model and the best model), and weight, representing the Akaike weight, signifying the level of support or evidence of a model being the most parsimonious among the candidate model set.

model	df	logLik	AICc	delta	wt
~ animal wt * seed wt + animal wt * seed wt	6	-81.8	175.7	0.0	0.7
~ animal wt * seed length + animal wt * seed length	6	-83.8	179.8	4.1	0.1
~ animal wt + pulp-seed ratio + animal wt * pulp-seed ratio	6	-84.2	180.5	4.8	0.1
~ animal wt + fruit skin width	5	-85.4	181.0	5.3	0.1
~ animal wt	4	-86.9	182.0	6.2	0.0
~ animal wt + fruit protection + animal wt * fruit protection	8	-84.6	185.5	9.8	0.0
~ animal wt + fruit protection	6	-86.7	185.7	10.0	0.0
~ animal wt + fruit skin width + animal wt * fruit skin width	6	-87.0	186.2	10.5	0.0
~ animal wt + seed length	5	-88.1	186.3	10.6	0.0
~ animal wt + seed wt	5	-88.2	186.5	10.7	0.0
~ animal wt + total no. of seeds	5	-88.3	186.7	11.0	0.0
~ animal wt + fruit length + animal wt * fruit length	6	-87.3	186.8	11.1	0.0
~ animal wt + pulp-seed ratio	5	-88.5	187.1	11.3	0.0
~ animal wt + fruit length	5	-88.6	187.4	11.7	0.0
~ animal wt + pulp wt	5	-88.9	187.8	12.1	0.0
~ animal wt + fruit wt	5	-88.9	188.0	12.3	0.0
~ animal wt + total seed wt	5	-89.1	188.4	12.7	0.0
~ animal wt + total seed wt + animal wt * total seed wt	6	-88.7	189.5	13.8	0.0
~ animal wt + total no. of seeds + animal wt * total no. of seeds	6	-88.7	189.7	14.0	0.0
~ animal wt + seed protection	7	-87.9	190.0	14.3	0.0
~ animal wt + pulp wt + animal wt * pulp wt	6	-89.2	190.7	15.0	0.0
~ animal wt + fruit wt + animal wt * fruit wt	6	-90.5	193.1	17.4	0.0
~ animal wt + edible tissue type	8	-89.0	194.4	18.7	0.0
~ animal wt + edible tissue type + animal wt * edible tissue type	12	-86.5	197.7	22.0	0.0
~ animal wt + seed protection + animal wt * seed protection	10	-89.8	200.1	24.4	0.0
~ animal wt + fruit crop	10	-91.7	203.9	28.2	0.0
~ fruit skin width	4	-103.2	214.6	38.9	0.0
~ 1	3	-104.9	215.9	40.2	0.0
~ animal wt + fruit crop + animal wt * fruit crop	16	-92.7	218.8	43.1	0.0
~ total no. of seeds	4	-105.6	219.3	43.5	0.0
~ fruit protection	5	-104.8	219.7	44.0	0.0
~ seed length	4	-106.2	220.4	44.7	0.0
~ seed wt	4	-106.2	220.5	44.8	0.0
~ pulp-seed ratio	4	-106.3	220.7	45.0	0.0
~ fruit length	4	-106.3	220.7	45.0	0.0
~ fruit wt	4	-106.8	221.6	45.9	0.0

~ pulp wt	4	-106.8	221.8	46.1	0.0
~ total seed wt	4	-107.1	222.2	46.5	0.0
~ seed protection	6	-105.8	223.9	48.2	0.0
~ edible tissue type	7	-107.1	228.4	52.7	0.0
~ fruit crop	9	-110.7	239.9	64.2	0.0

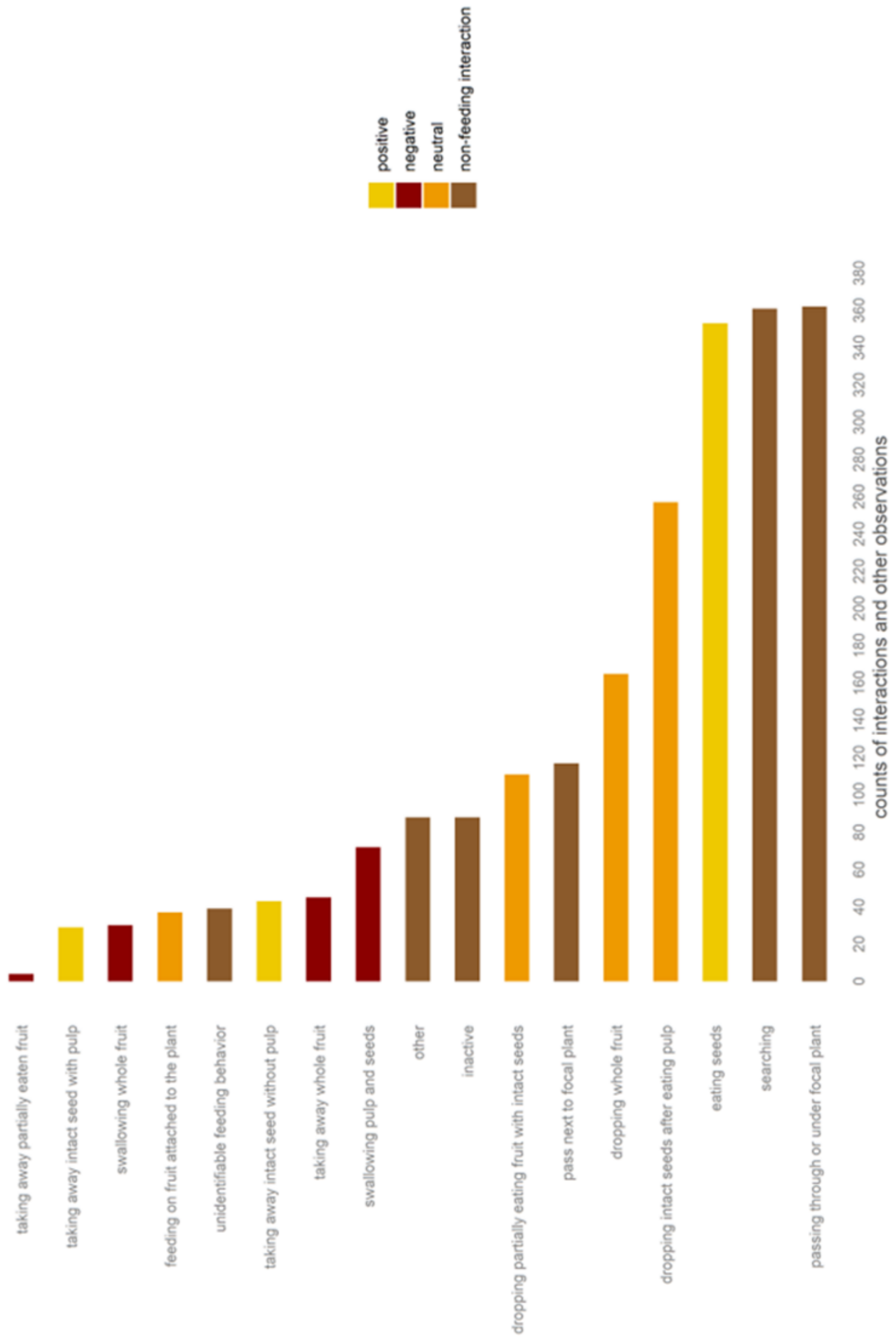
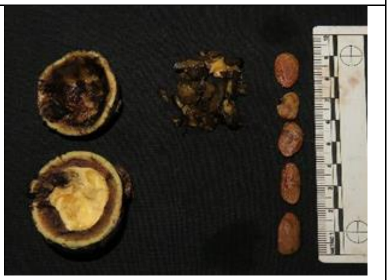
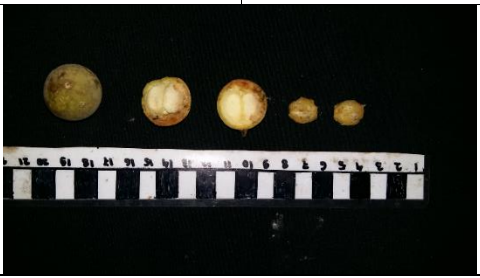


Figure A2.1. Counts of different feeding interactions and non-feeding events.

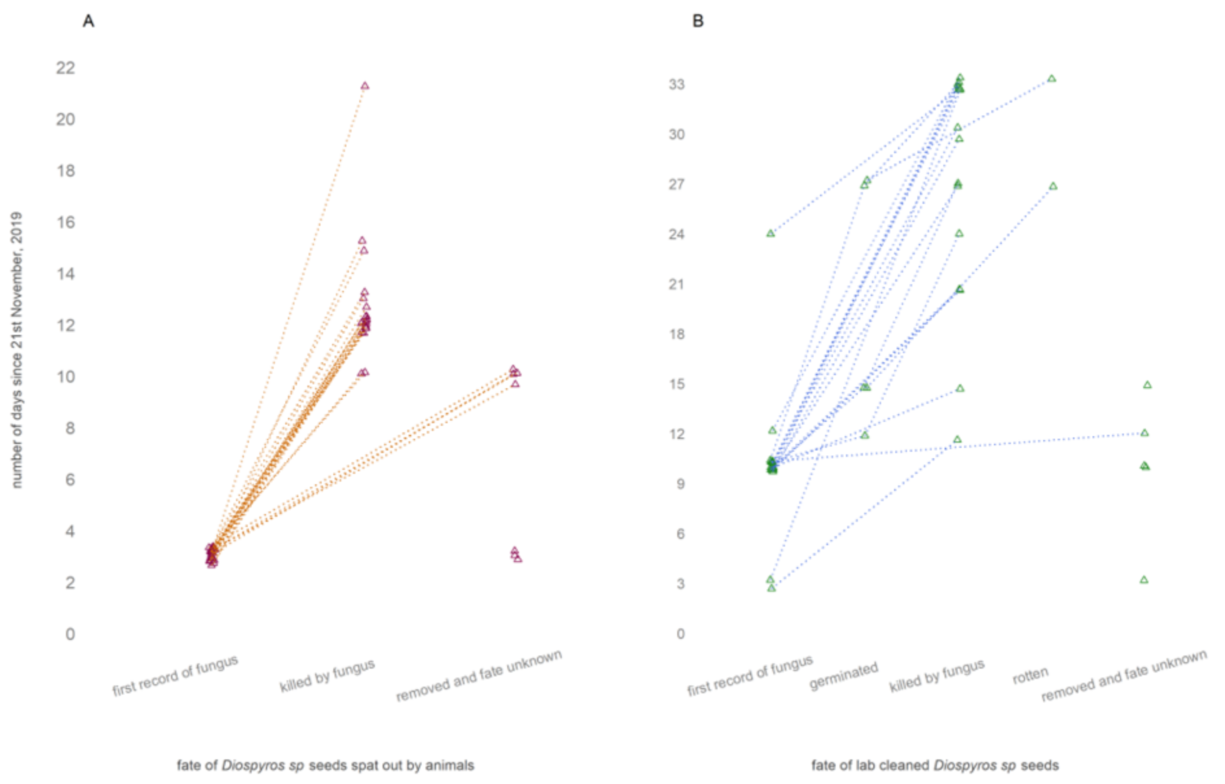
Appendix B: Supplementary Boxes, Tables, and Figures for Chapter 3

Box B3.1. Photographs of seeds from large-seeded trees and lianas for which we experimentally assessed post-dispersal seed fate.

	
Canarium sp. 1	*Canarium* sp. 2
	
Diospyros sp.	*Dracontomelon costatum*
	
Irvingia malayana	*Lansium domesticum*
	
Madhuca sp.	*Palaquium* sp.
	

Parartocarpus sp.	*Strychnos* sp.1
	
Strychnos sp.2	*Willughbeia* sp.1
	
Willughbeia sp.2	*Willughbeia* sp.3
	
Xanthophyllum sp.	

Box B3.2. Overview of the results obtained from a short-term study investigating the fate of 51 *Diospyros sp.* seeds as detailed in the final panel. Panel A presents data on seeds spat out by animals, showcasing the diversity of their outcomes. In panel B, we observe the outcomes of seeds that were cleaned at our lab. Panel C includes a photograph of a tagged seed expelled by animals, while panel D depicts a seed under fungal attack after being spat out by animals.



C

D

In this study, we tracked the fate of 51 *Diospyros* sp. seeds from a single individual plant. The seeds were categorized into two distinct groups: those spat out by long-tailed macaques and Bornean orangutans (referred to as AS, n=27) and those cleaned in our lab (referred to as LC, n=24). These seeds were distributed across various distances from the parent plant (under the parent plant, 25m away, and 50m away) and at different seed densities (low=1 seed, medium=5 seeds, and high=10 seeds). High-density seed stations consisted of 5 AS and 5 LC seeds, while medium-density stations contained 3 AS and 2 LC seeds. Low-density stations were established separately for AS and LC seeds. It is worth noting that AS seeds retained fruit pulp on their seed coat (panel C), while LC seeds were devoid of any fruit pulp. Seed fate was monitored as described in the methods section (section 3.3.1).

Fungal presence (panel D) was observed in all AS seeds on the first sampling occasion, which occurred on day 3 (panel A). Subsequently, it took an average of 12.7 days (with a range of 12 to 21 days and a standard deviation of 2.24) for 20 of the AS seeds to succumb to fungal predation (panel A). The fate of the remaining 7 seeds could not be ascertained as they were removed and subsequently became untraceable.

In contrast, LC seeds exhibited fungal presence on day 3 (n=1), day 10 (n=14), day 12 (n=1), and day 24 (n=1) (panel B). Among LC seeds, five germination events were recorded, including three seeds that already exhibited fungal presence. The germinated seeds took an average of 19.2 days (with a standard deviation of 5.9) to sprout. Of the LC seeds, 17, including three of the germinated seeds, succumbed to fungal predation after an average of 27.7 days (ranging from 12 to 33 days, with a standard deviation of 6.6) (panel B). Two germinated seeds perished on day 27 and day 33 from unknown causes. The fate of the remaining five seeds could not be determined as they were removed and subsequently untraceable.

In summary, our findings reveal that AS *Diospyros* sp. seeds were more vulnerable to fungal attacks and had a shorter lifespan compared to lab-cleaned seeds. This suggests that endozoochory involving seed scarification could be advantageous. However, the presence of seed disperser biology, the presence of fecal matter, and microsite conditions where seeds arrive can all differently influence seed fate (Traveset et al.,, 2007). Notably, no instances of germination were observed for AS seeds. It is also noteworthy that the demise of seeds that managed to survive longer was expedited due to a flooding event following exceptionally heavy rainfall when seeds were submerged for at least 2 whole days.

Reference: Traveset, A. A. J. A., Robertson, A. W., and Rodríguez-Pérez, J. (2007). A review on the role of endozoochory in seed germination. *Seed dispersal: theory and its application in a changing world*, 78-103.

Table B3.1. Overview of the combined count of seeds predated upon by different seed predators for each large-seeded plant species in our study.

Plant species/ **Seed predator**	**Number killed**	**Seed protection**	**Average weight (grams)**	**Average Length (mm)**
Canarium sp. 1		stone	6.15	41.29
Bearded pigs	6			
Three-striped ground squirrels	9			
Rats	8			
Unknown vertebrates	6			
Canarium sp. 2		stone	12.05	63.58
Tufted ground squirrels	12			
Three-striped ground squirrels	1			
Unknown vertebrates	4			
Unknown causes	1			
Diospyros sp. 1		hard	2.02	25.69
Fungi	72			
Unknown vertebrates	1			
Unknown causes	3			
Dracontomelon costatum		stone	3.09	18.59
Tufted ground squirrels	11			
Bearded pigs	1			
Rats	5			
Irvingia malayana		hard	14.15	39.1
Bearded pigs	47			
Unknown invertebrates	9			
Ants	10			
Three-striped ground squirrels	4			
Beetles	3			
Tufted ground squirrels	1			
Unknown vertebrates	1			
Worms	3			
Unidentified larvae	2			
Fungi	1			
Unknown causes	2			
Lansium domesticum		soft	2.05	19.53
Unknown invertebrates	3			
Rats	5			
Unknown vertebrates	2			
Madhuca sp.		soft	2.19	27.08
Bearded pigs	31			
Unknown vertebrates	3			
Unknown causes	1			
Parartocarpus sp.		hard	2.48	19.66

Red langurs	16			
Bearded pigs	11			
Ants	8			
Unknown invertebrates	3			
Rats	2			
Palaquium sp.		hard	2.1	28.84
Rats	2			
Unknown vertebrates	2			
Strychnos sp. 1		hard	0.53	16.56
Rats	23			
Bearded pigs	11			
Three-striped ground squirrels	1			
Ants	2			
Unknown vertebrates	4			
Unknown invertebrates	3			
Strychnos sp. 2		hard	0.92	19.05
Fungi	15			
Rats	10			
Unknown vertebrates	3			
Unknown invertebrates	2			
Worms	2			
Ants	1			
Willughbeia sp. 1		soft	8.45	36.45
Bearded pigs	24			
mouse deer	11			
Bornean crested firebacks	4			
Unknown vertebrates	4			
Willughbeia sp. 2		soft	2.45	22.9
Unknown invertebrates	6			
Unknown vertebrates	3			
Rats	3			
Bearded pigs	4			
Bornean crested firebacks	1			
Willughbeia sp. 3		soft	1.83	20.1
Bearded pigs	18			
mouse deer	2			
Three-striped ground squirrels	3			
Rats	3			
Unknown invertebrates	3			
Unknown vertebrates	2			
Unknown causes	2			
Xanthophyllum sp. 1		hard	1.33	14.64
Ants	23			

Unknown invertebrates	4			
Fungi	1			
Unknown causes	2			

Table B3.2. Comparison of Generalized Linear Mixed Models used to evaluate the influence of density (categorized as low=1 seed, medium=5 seeds, and high=10 seeds), distance (categorized as 0m away from the parent plant, 25m, and 50m away), and seed traits (weight, volume, length, and protection) on the probability of predation by vertebrates (a binary variable given as VP in the table). Seed protection was categorized as soft (capable of being broken by fingernail), hard (resistant to breakage by fingernail), and stone (seeds with true stones). The table includes key model comparison metrics such as log-likelihood (logLik), corrected Akaike Information Criterion (AICc), delta (the difference in AICc between the model and the best model), and weight, representing the Akaike weight, signifying the level of support or evidence of a model being the most parsimonious among the candidate model set.

model	**df**	**logLik**	**AICc**	**delta**	**weight**
VP ~ density + distance + density * distance	10	-296.12	612.55	0.00	0.84
VP ~ density + distance	6	-301.90	615.91	3.37	0.16
VP ~ distance	4	-308.55	625.17	12.62	0.00
VP ~ distance + weight	5	-307.84	625.77	13.23	0.00
VP ~ distance + protection	6	-306.87	625.85	13.31	0.00
VP ~ distance + volume	5	-308.09	626.27	13.73	0.00
VP ~ distance + length	5	-308.41	626.90	14.35	0.00
VP ~ density + volume	5	-321.06	652.20	39.65	0.00
VP ~ density + weight	5	-321.94	653.97	41.42	0.00
VP ~ density	4	-323.38	654.82	42.27	0.00
VP ~ density + protection	6	-321.59	655.30	42.75	0.00
VP ~ density + length	5	-322.66	655.40	42.86	0.00
VP ~ volume	3	-329.41	664.85	52.31	0.00
VP ~ 1	2	-330.53	665.07	52.53	0.00
VP ~ weight	3	-329.66	665.35	52.80	0.00
VP ~ protection	4	-328.76	665.58	53.03	0.00
VP ~ volume + protection	5	-327.99	666.06	53.52	0.00
VP ~ weight + protection	5	-328.10	666.28	53.74	0.00
VP ~ length	3	-330.18	666.40	53.85	0.00
VP ~ length + protection	5	-328.70	667.48	54.93	0.00
VP ~ weight + protection + weight * protection	7	-326.86	667.89	55.34	0.00
VP ~ volume + protection + volume * protection	7	-327.76	669.68	57.14	0.00
VP ~ length + protection + length * protection	7	-328.42	671.00	58.45	0.00

Table B3.3. Comparison of Generalized Linear Mixed Models used to evaluate the influence of density (categorized as low=1 seed, medium=5 seeds, and high=10 seeds), distance (categorized as 0m away from the parent plant, 25m, and 50m away), and seed traits (weight, volume, length, and protection) on the probability of caching or predation by scatter hoarders (a binary variable given as CP in the table). Seed protection was categorized as soft (capable of being broken by fingernail), hard (resistant to breakage by fingernail), and stone (seeds with true stones). The table includes key model comparison metrics such as log-likelihood (logLik), corrected Akaike Information Criterion (AICc), delta (the difference in AICc between the model and the best model), and weight, representing the Akaike weight, signifying the level of support or evidence of a model being the most parsimonious among the candidate model set.

model	**df**	**logLik**	**AICc**	**delta**	**weight**
CP ~ distance + weight	5	-137.16	284.56	0.00	0.64
CP ~ distance	4	-140.05	288.26	3.70	0.10
CP ~ distance + length	5	-139.02	288.28	3.72	0.10
CP ~ distance + volume	5	-139.33	288.92	4.36	0.07
CP ~ density + distance	6	-138.85	290.05	5.49	0.04
CP ~ distance + protection	6	-139.17	290.69	6.13	0.03
CP ~ length + protection + length * protection	7	-140.16	294.79	10.23	0.00
CP ~ weight + protection + weight * protection	7	-140.52	295.50	10.94	0.00
CP ~ density + distance + density * distance	10	-137.30	295.54	10.98	0.00
CP ~ weight + protection	5	-143.38	297.01	12.45	0.00
CP ~ volume + protection + volume * protection	7	-142.40	299.27	14.71	0.00
CP ~ weight	3	-148.52	303.14	18.58	0.00
CP ~ length + protection	5	-147.71	305.67	21.11	0.00
CP ~ density + weight	5	-147.79	305.82	21.26	0.00
CP ~ 1	2	-151.13	306.30	21.74	0.00
CP ~ volume + protection	5	-148.05	306.34	21.78	0.00
CP ~ protection	4	-149.47	307.10	22.54	0.00
CP ~ length	3	-150.52	307.13	22.57	0.00
CP ~ volume	3	-150.87	307.84	23.28	0.00
CP ~ density	4	-150.40	308.96	24.39	0.00
CP ~ density + protection	6	-148.68	309.72	25.16	0.00
CP ~ density + length	5	-149.74	309.72	25.16	0.00
CP ~ density + volume	5	-150.09	310.43	25.87	0.00

Table B3.4. Comparison of Generalized Linear Mixed Models used to evaluate the influence of density (categorized as low=1 seed, medium=5 seeds, and high=10 seeds), distance (categorized as 0m away from the parent plant, 25m, and 50m away), and seed traits (weight and protection) on the probability of caching or predation by scatter hoarders (a binary variable given as CP in the table). Seed protection was categorized as soft (capable of being broken by fingernail), hard (resistant to breakage by fingernail), and stone (seeds with true stones). The table includes key model comparison metrics such as log-likelihood (logLik), corrected Akaike Information Criterion (AICc), delta (the difference in AICc between the model and the best model), and weight, representing the Akaike weight, signifying the level of support or evidence of a model being the most parsimonious among the candidate model set.

model	**df**	**logLik**	**AICc**	**delta**	**weight**
CP ~ distance + weight	5	-137.16	284.56	0.00	0.78
CP ~ distance	4	-140.05	288.26	3.70	0.12
CP ~ density + distance	6	-138.85	290.05	5.49	0.05
CP ~ distance + protection	6	-139.17	290.69	6.13	0.04
CP ~ weight + protection + weight * protection	7	-140.52	295.50	10.94	0.00
CP ~ density + distance + density * distance	10	-137.30	295.54	10.98	0.00
CP ~ weight + protection	5	-143.38	297.01	12.45	0.00
CP ~ weight	3	-148.52	303.14	18.58	0.00
CP ~ density + weight	5	-147.79	305.82	21.26	0.00
CP ~ 1	2	-151.13	306.30	21.74	0.00
CP ~ protection	4	-149.47	307.10	22.54	0.00
CP ~ density	4	-150.40	308.96	24.39	0.00
CP ~ density + protection	6	-148.68	309.72	25.16	0.00

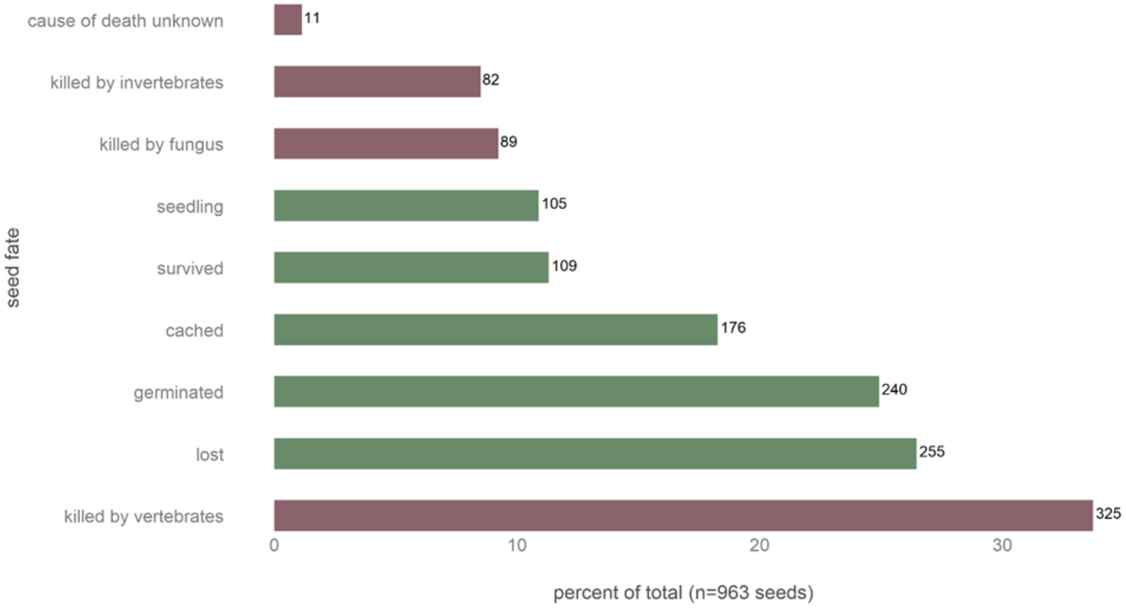


Figure B3.1. Distribution of seed fate events (including death, germination, loss, seedling establishment, and survival until the end of the study) as a percentage of the 963 seeds that were sampled. Red bars indicate seed death events, while green bars represent all other events.

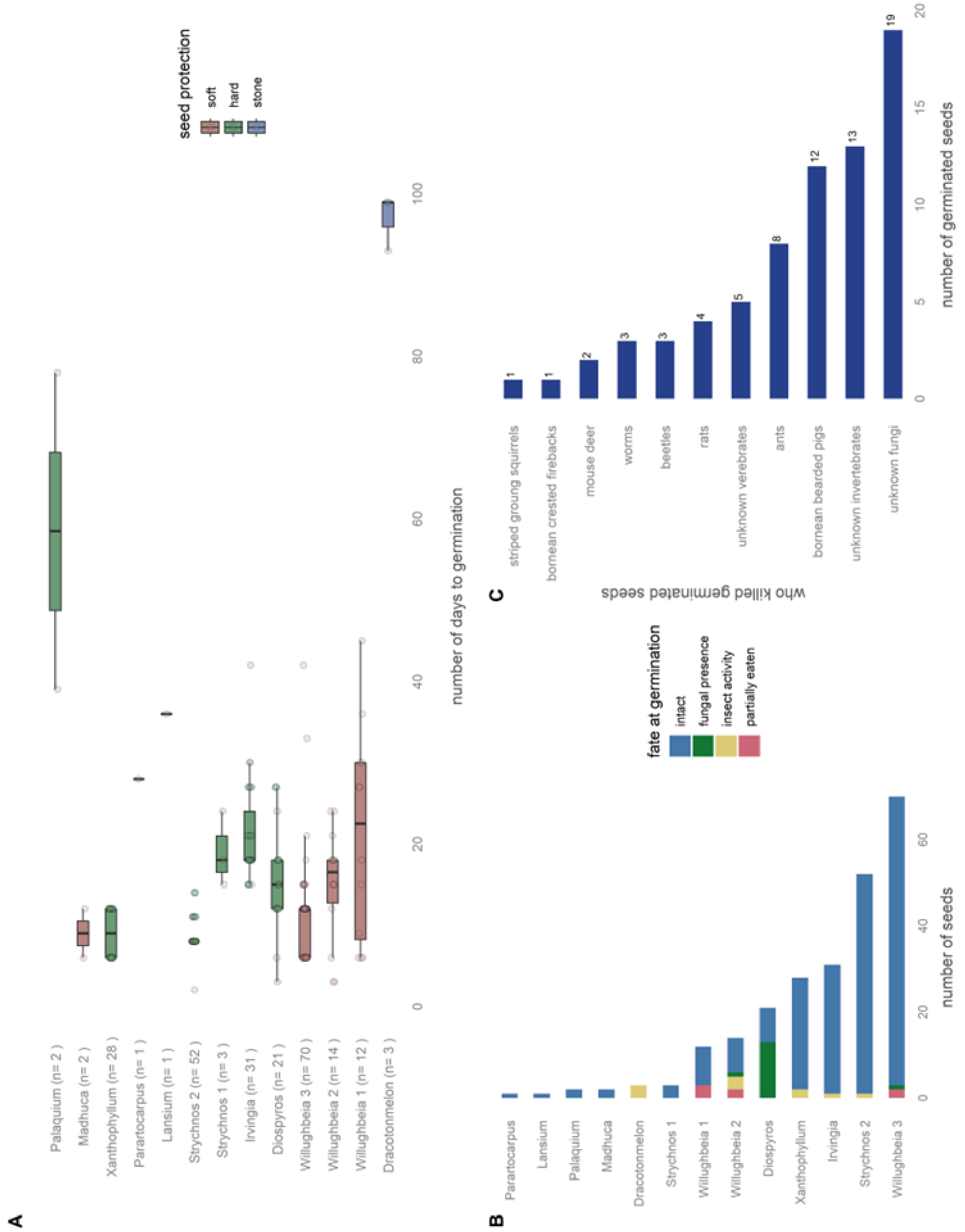


Figure B3.2. Germination events. Panel A displays the time taken for germination in cases where germination was recorded. Panel B presents the count of seeds in various states (intact, fungal presence, insect activity, and partially eaten) at the initial observation of germination. Panel C highlights the count of germinated seeds that were subsequently preyed upon by seed predators.

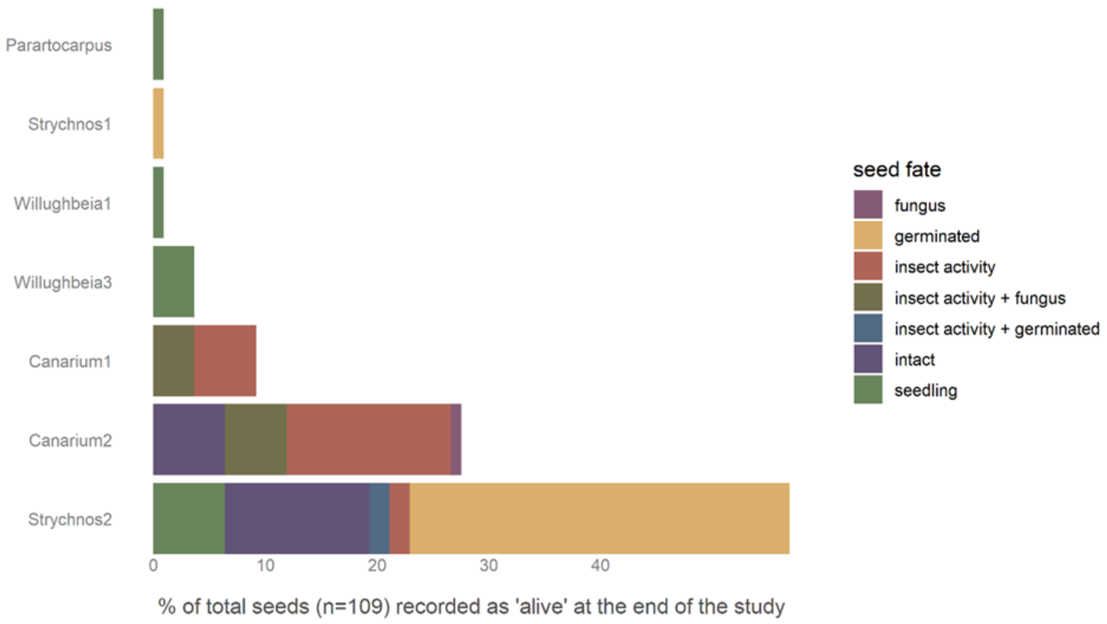


Figure B3.3. Percentage of surviving seeds in different states at the conclusion of the study.

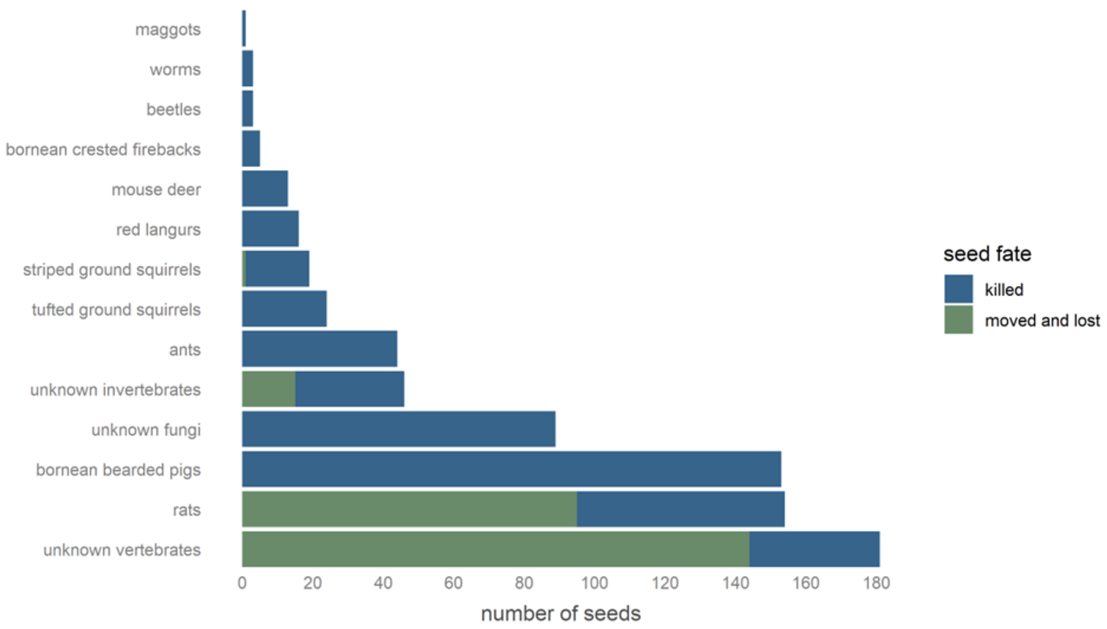


Figure B3.4. Count of seeds that were either killed or moved and subsequently lost due to seed predators.

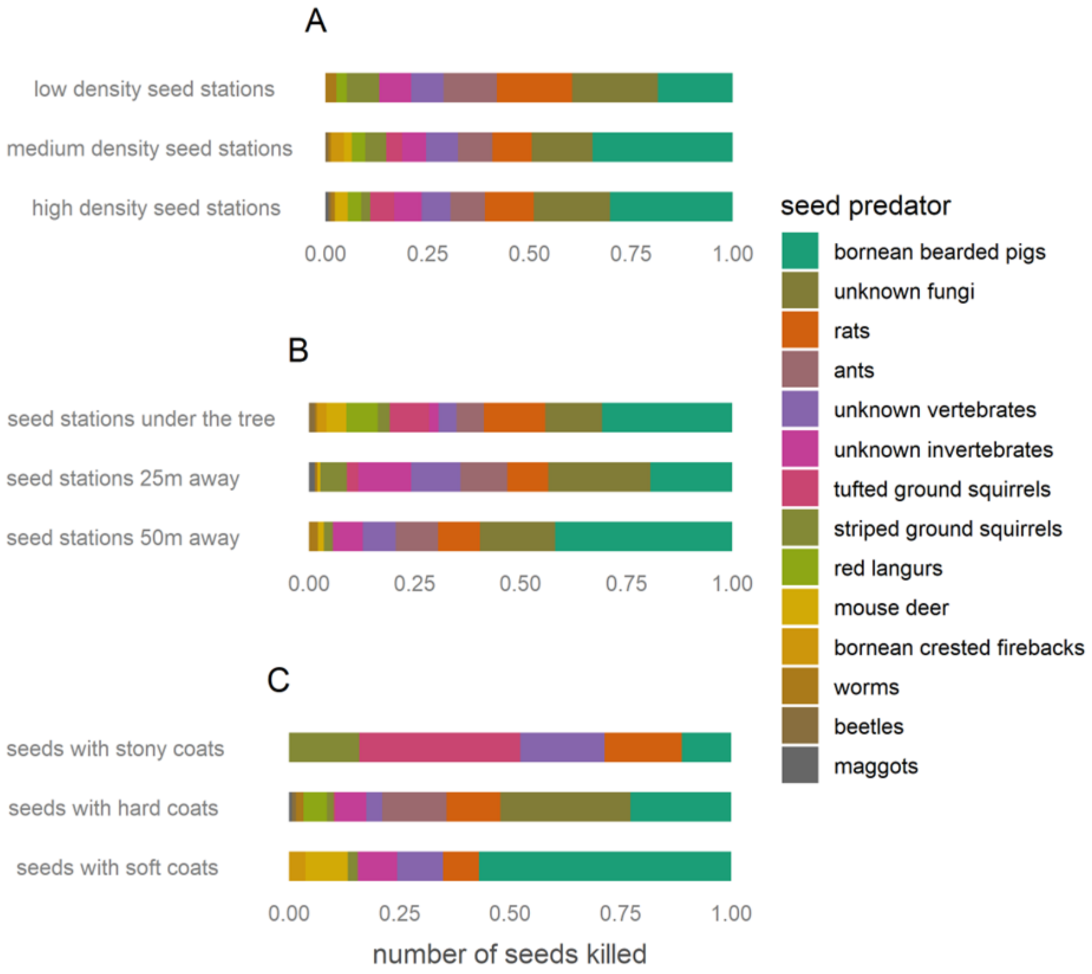


Figure B3.5. Proportion of seeds within low, medium, and high-density seed stations (Panel A), within seed stations located at the parent plant, 25m away, and 50m away (Panel B), and with soft, hard, stony coats (Panel C) that were preyed upon by seed predators.

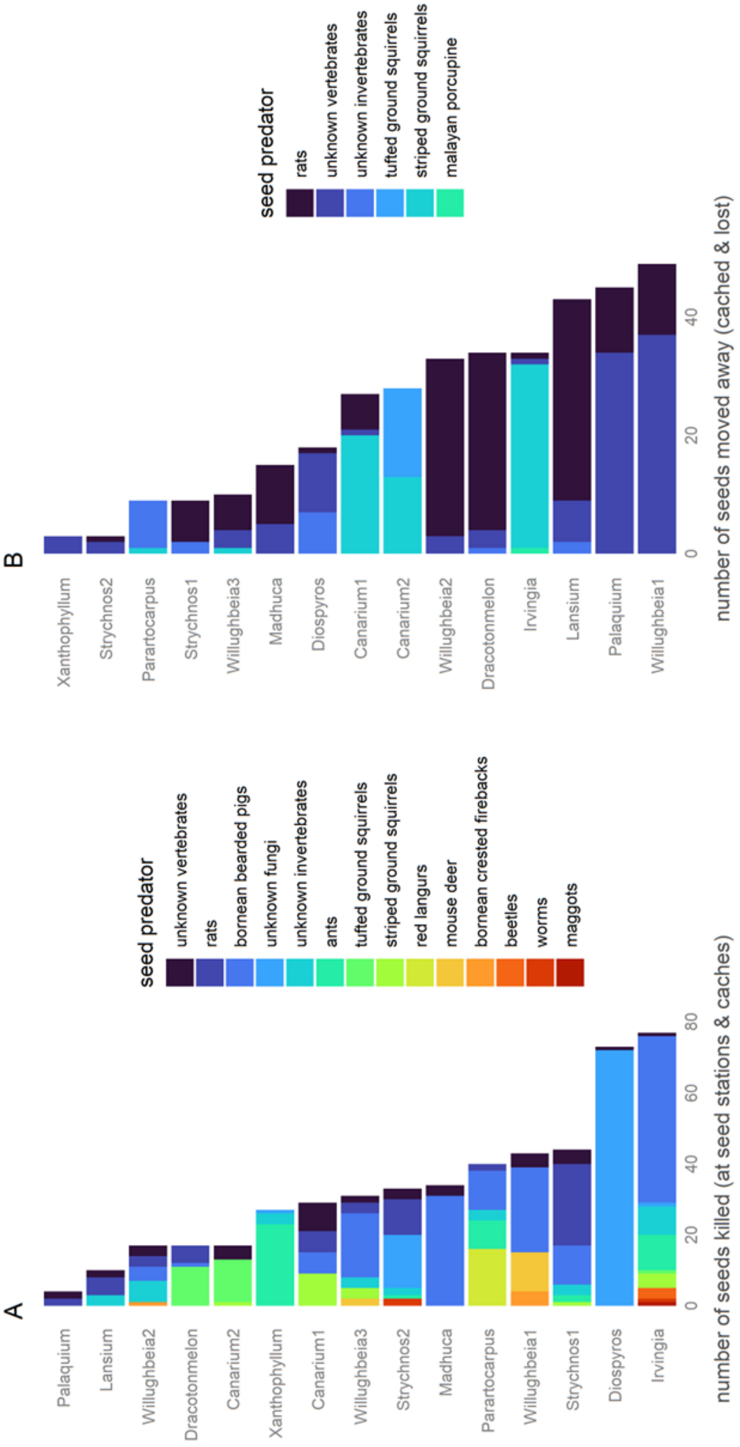


Figure B3.6. Number of seeds across large-seeded plant species that were killed (within seed stations and from caches; Panel A) and the proportion that were moved (including those that were cached and those moved and subsequently lost; Panel B) by various seed predators.

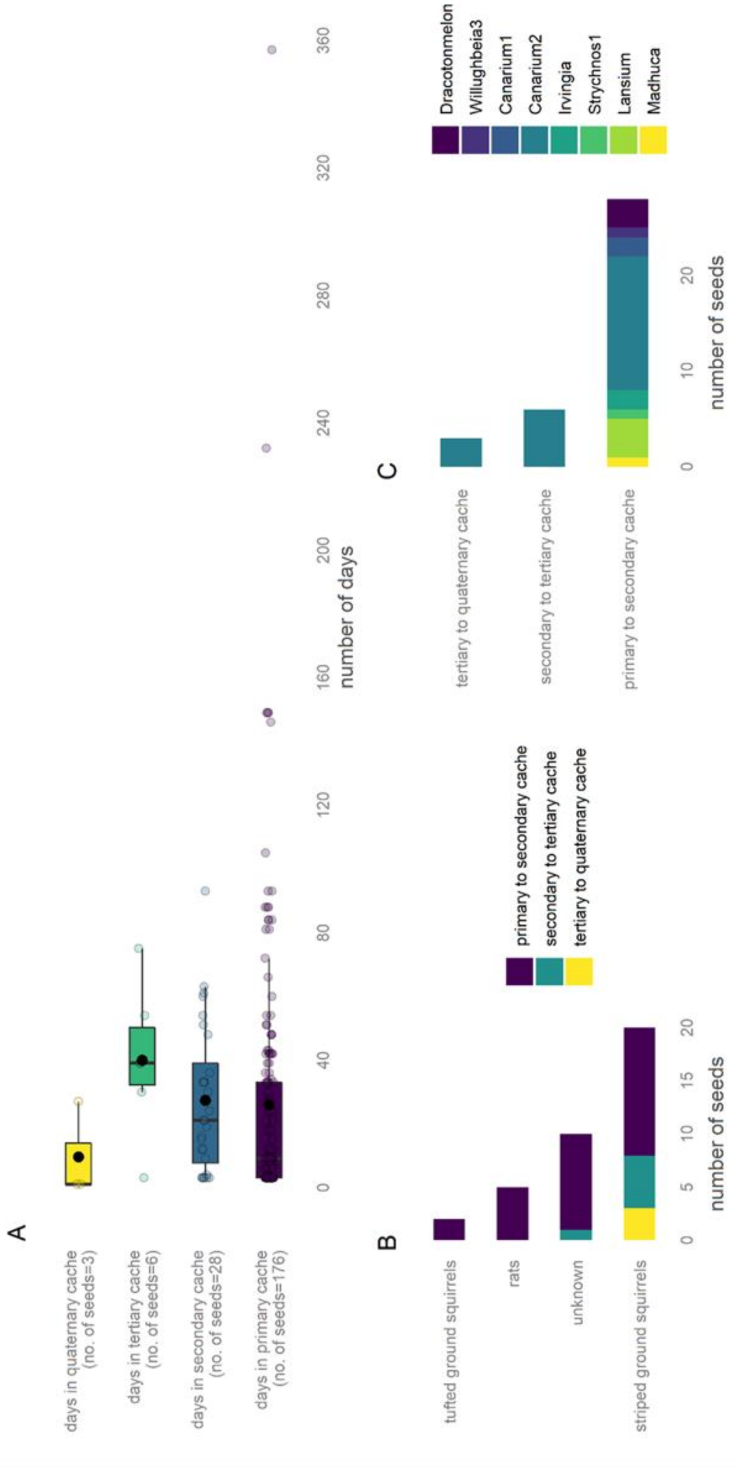


Figure B3.7. Duration (in days) that seeds were retained in primary, secondary, tertiary, and quaternary caches (Panel A). Panel B represents the count of seeds moved from primary to secondary, secondary to tertiary, and tertiary to quaternary caches by various scatter hoarders. Panel C depicts the count of seeds from different plant species that were moved from primary to secondary, secondary to tertiary, and tertiary to quaternary caches.

Appendix C: Supplementary Boxes, Tables, and Figures for Chapter 4

Box C4.1. Verbal consent procurement statement for participant recruitment in our study.

Bahasa Indonesia	
“Halo, ini Swapna. Dia adalah seorang mahasiswa PhD di Universitas Michigan, AS. Saya Putri, saya mahasiswa di Universitas Nasional, Jakarta. Kami tertarik untuk belajar tentang pengetahuan tradisional dan penggunaan sumber daya hutan saat ini. Kami sedang melakukan penelitian untuk memahami praktik perburuan saat ini. Beberapa tujuan dari penelitian ini untuk memahami hewan liar apa yang Anda suka untuk berburu, seberapa sering dan di mana anda berburu, tujuan berburu, senjata yang digunakan untuk berburu, dan apakah anda merasa populasi hewan liar berubah. Kami akan menanyakan beberapa pertanyaan tentang ini. Anda dapat menolak untuk menjawab pertanyaan kami. Orang yang tinggal di dekat Taman Nasional Gunung Palung diharapkan untuk berpartisipasi dalam penelitian ini. Menjadi bagian dalam penelitian ini berlangsung selama satu jam tiga puluh menit dan mungkin termasuk satu atau dua kunjungan. Tidak ada risiko yang terkait dengan penelitian ini, karena kami tidak akan mencatat nama Anda atau mengumpulkan informasi apa pun yang dapat mengungkapkan identitas Anda seperti foto, alamat, nomor telepon, dll. Jika kami mengetahui tentang risiko apa pun nanti, kami akan beri tahu Anda apa mereka dan Anda dapat menentukan apakah Anda ingin terus berpartisipasi dalam penelitian ini. Partisipasi Anda sepenuhnya bersifat sukarela. Anda tidak akan menerima uang atau manfaat lain apa pun untuk mengambil bagian dalam studi penelitian ini. Anda dapat memilih untuk tidak mengambil bagian dalam studi penelitian ini dan dapat memilih keluar dari studi ini kapan saja. Tolong catat nomor saya. Anda dapat menghubungi saya kapan saja jika Anda ingin kami tidak menggunakan data yang kami kumpulkan dari Anda. Apakah Anda bersedia berpartisipasi dalam studi ini? Apakah tidak apa-apa jika kami menanyakan beberapa pertanyaan? Apakah saya bisa merekam audio dari wawancara ini? Terima kasih banyak."	“Hello, this is Swapna. She is a PhD student at the University of Michigan, USA. I am Putri, I am a student at Universitas Nasional, Jakarta. We are interested in learning about traditional knowledge and the current use of forest resources. We are carrying out research to understand current practices of hunting. Some of the goals of this study are to understand what wild animals you prefer to hunt, how often and where you hunt, your purpose of hunting, weapons used for hunting, and if you feel populations of wild animals are changing. We will ask you a few questions about this. You may refuse to answer our questions. People living close to Gunung Palung National Park are expected to participate in this study. Taking part in this study may last for an hour and thirty minutes and may include one or two visits. There is no risk associated with this study, since we will not take your name or collect any information that could reveal your identity such as your photo, address, phone number, etc. If we learn about any risks later, we will let you know what they are, and you may decide if you want to continue participating in the study. Your participation is completely voluntary. You will not receive any money or any other benefits for taking part in this research study. You may choose not to take part in this research study and can opt out of the study at any time. Please take my number. You can call me any time if you want us to not use the data, we collected from you. Are you willing to participate in this study? Would it be alright if we asked you a few questions? Is it okay if we record audio from this interview? Thank you so much.”

Box C4.2. Structure of questionnaire used to collect demographic and socioeconomic information, along with information on hunting patterns, meat consumption, preferences, beliefs, and perceptions.

Section 1: Demographic and socioeconomic information

1. Interviewee ID (number assigned to the interviewee)

2. Age / *Usia* (number)

3. Education / *Pendidikan* [(0) none, (1) primary school / *SD*, (2) secondary school / *SMP*, (3) high school / *SMA* & (4) beyond high school]

4. Name of village / *Nama desa* (three letter village code)

5. Ethnic group / *Kelompok etnis* / Tribe / Suku (open)

6. Number of members in the household / *jumlah anggota keluarga* (number)

7. Occupation & primary source of income / *pekerjaan dan sumber pemasukan utama* (if more than three list top three)

8. Number of working members in the household / *jumlah anggota keluarga yg bekerja* (number)

9. Does your household use fuelwood or gas? / *di rumah pakai bahan bakar kayu atau gas* [(0) Fuelwood, (1) Gas, (2) Both]

10. Type of house / *Tipe rumah* [(0) wood, (1) semi-permanent (wood & cement), (2) permanent (cement)]

11. House roof type / *Tipe atap rumah* [(0) thatch, (1) wood, (2) tiles, (3) metal sheet]

12. Number of rooms / *jumlah kamar* (1, 2, or 3+)

13. Number of houses owned / *jumlah rumah yang dimiliki* (number)

14. Possession of land / *kepemilikan tanah* (y/n)

If y, 14.1. how much / *berapa luas* (number)

14.2. utilization of land / *pemanfaatan tanah* [(0) none, (1) agriculture / *pertanian* (crop/s), (2) plantation / *perkebunan* (crop), (3) lease / *sewa* (used for), (4) home, (5) other (list)]

15. Possession of domestic animals / *Kepemilikan hewan domestik* (y/n)

If y, 15.1. type of animal / *Tipe hewan* (open) & number / *jumlah* (number)

16. List (up to) three basic facilities that you feel are severely lacking and need attention in your village / *Sebutkan hingga 3 fasilitas dasar yang anda rasa sangat kurang dan perlu perhatian di desa Anda*

Section 2: Hunting patterns, meat consumption and preferences

1. Father is/was a hunter? / *apakah bapak anda pemburu?* (y/n)

2. How many members in your household currently hunt? */ berapa anggota keluarga yang berburu?* (number)

3. How long have you been hunting? */ sudah berapa lama berburu?* (number)

4. How often do you hunt? */ berapa sering anda berburu?* [(0) 1–5 times in your lifetime / 1-5 *kali selama hidup*, (1) 1–2 times/year, (2) 1–2 times/ 6 month, (3) 1–2 times/month or (4) 1–2 times/week or daily]

5. Why do you hunt? / *kenapa berburu?* [(0) home consumption / *konsumsi*, (1) money / *uang*, (2) cultural/religious reasons / *budaya-keagamaan*, (3) sport, hobby / *olahraga*, (4) crop defense / *pertahanan*, (5) medicine / *obat*, (6) other (list)] choose all that apply in order of importance

6. How often do you consume wildmeat? / *berapa sering anda konsumsi daging liar* [(0) never, (1) 1–5 times in your lifetime / 1-5 *kali selama hidup*, (2) 1–2 times/year, (3) 1–2 times/ 6 month, (4) 1–2 times/month or (5) 1–2 times/week or daily]

7. Do you sell wildmeat? (y/n). How often? / *Anda menjual daging liar? Berapa sering anda menjual daging liar* [(0) never, (1) 1–5 times in your lifetime / 1-5 *kali selama hidup*, (2) 1–2 times/year, (3) 1–2 times/ 6 month, (4) 1–2 times/month or (5) 1–2 times/week or daily]

8. Apart from the ones you listed previously are there any other wild animals that you prefer? Maybe species that were not shown in the photographs. / *Terlepas dari daftar sebelumnya, apa ada hewan liar lain yang anda inginkan? Mungkin jenis hewan yang tidak ada di foto-toto tersebut.*

9. In general, what is the most commonly used hunting technique? / *secara umum, teknik buru apa yang paling sering digunakan?* [(0) gun / *senapan*, (1) trap & snares / *perangkap dan jerat*, (2) machete / *golok*, (3) bow & arrow / *panah*, (4) catapult / sling shot / *ketapel*, (5) dog, (6) other (describe)]

10. Where do you commonly hunt? *Dimana anda biasa berburu?* [(0) farm (plantation/agricultural fields, (1) forest, (2) both] If forest, what is the name of the forest? / *nama hutanya?*

11. Hunting season / *Musim berburu* [(0) wet / *basah*, (1) dry / *kering*, (2) all year / *setiap tahun*, (3) other(describe)]

12. Estimate the time it usually takes, from leaving your home, to reach the hunting site / *Perkirakan waktu yang dibutuhkan, mulai dari meninggalkan rumah, hingga di lokasi berburu* [(0) > 2hrs, (1) half a day or 4-6 hrs, (2) a day 6-12 hrs, (3) more than a day <12 hrs]

13. When on hunting trips do you sleep in the forest? / *saat dalam perjalanan berburu apakah anda tidur di hutan?* [(0) never / *Tidak pernah*, (1) rarely / *Jarang*, (2) often / *sering*, (3) always]

14.

14.1. When did you hunt most recently? / *Kapan Anda terakhir berburu?* (open)

14.2. How many members were in your hunting group? *Ada berapa orang di kelompok berburu?* (number)

14.3. Where did you hunt? *Di mana Anda berburu?* (open)

14.4. What did you catch? *Apa yang anda buru?* (open)

14.5. What methods did you use? *Teknik berburu apa yang Anda gunakan* [(0) gun / *senapan*, (1) trap, net & snares / *perangkap, jaring & jerat*, (2) machete / *golok*, (3) bow & arrow / *panah*, (4) catapult / sling shot / *ketapel*, (5) dog */ Anjing*, (6) other (describe)]

14.6. What was done with the catch? *Apa yang anda lakukan dengan hewan itu?* (open)

15. How often do you consume domestic meat? / *berapa sering anda konsumsi daging domestik?* [(0) never, (1) 1–5 times in your lifetime / 1-5 *kali selama hidup*, (2) 1–2 times/year, (3) 1–2 times/ 6 month, (4) 1–2 times/month or (5) 1–2 times/week or daily]

15.1. If 0, why? / *kenapa*? [(0) expensive, (1) not easily available, (2) expensive and not easily available, (3) other]

16. Most preferred domesticated animals / *Sebutkan hewan domestik yang paling diminati* (list top 3; open)

17. What do you prefer, wild meat or domestic meat? / *anda lebih pilih apa, daging domestik atau daging liar?* [(0) wildmeat, (1) domestic meat)]

9.a. Why? (open)

18. Are there any local taboos or laws against killing and/or consuming certain wild animals? / *apa ada hal tabu atau aturan yang melarang membunuh atau konsumsi hewan liar tertentu?* (y/n; If y, provide examples)

19. Are wild animals used for cultural/religious purposes (Ramadan, Christmas, New year, wedding, birth, etc.)? / *apakah hewan liar digunakan untuk tujuan budaya atau keagamaan?* (y/n; If y, provide examples)

20. Are wild animals used for medicinal purposes? / *apakah hewan liar digunakan untuk tujuan pengobatan?* (y/n; If y, provide examples)

21. In your opinion, is hunting becoming more difficult? / *menurut anda, apa berburu jadi sulit dilakukan?* (y/n)

21.a. If y, [(0) low animal populations / *populasi hewan menurun*, (1) long travel time / *waktu perjalanan panjang* (2) increase in number of hunters from other areas / *jumlah pemburu meningkat di area itu*, (3) other(describe)] choose all that apply

22. If you think wild animals are becoming rare, does it worry you? Why? / *jika menurut anda hewan liar jadi langka, apa ini membuat anda khawatir? Kenapa?* (y/n, open)

23. Do you know if hunting is illegal? / *apa anda tahu berburu itu illegal?* (y/n)

    23.1. Do you think hunting is risky / *apa berburu itu beresiko?* (y/n)

    23.2. If y or n, why do you think it is or it isn’t risky? / *kenapa menurut anda itu beresiko atau tidak beresiko?* (open)

24. Do you want to continue to hunt? / apa anda ingin terus berburu? (y/n)

    24.1. Why or why not? / *Kenapa atau kenapa tidak?* (open)

25. Do you have children? / *Apa anda punya anak?* (y/n)

    25.1. Would you be happy if your children participated in hunting? / *Apa anda senang jika anak anda ikut berburu?* (y/n)

    25.2. Why or why not? / *Kenapa atau kenapa tidak?* (open)

Box C4.1. Anecdotal account of sun bear gallbladder medicinal use rooted in folklore.

The medicinal use of bear gallbladders finds its roots in local folklore that has been passed down through generations. The story recounts instances of injured bears experiencing miraculous recoveries. These tales narrate accounts of bears tumbling from trees, crashing hard onto the forest floor, and losing consciousness. Naturally, those witnessing such falls assumed that the bears must have suffered grievous internal injuries. However, much to their astonishment, the fallen bears soon regained consciousness, showing no signs of harm. Undeterred by the fall, the bears continued going about their day seemingly unscathed. This extraordinary recovery was attributed to the rupturing of the gallbladder from the fall, which they believed held a reservoir of potent healing properties. Upon rupturing, healing bile would be released, flowing through the bear's body, repairing internal wounds, and restoring its strength. Thus, it came to be believed that crafting medicine from bear gallbladders could treat internal injuries sustained from falling with remarkable efficacy.

Image source: Hinson, L. Teddy Bear Climbing A Tree Drawing [Image]. Retrieved from https://pixy.org/4710908 on 2nd September 2023. Creative Commons CC0 License.

Table C4.1. List of 33 fruit-and seed-eating mammal and large bird species included in this study, featuring their scientific, common, and local names, with body weight (kg) denoted as midpoints for weight ranges and gender variations. Additionally, it presents the current IUCN Status/Population trend data retrieved from https://www.iucnredlist.org/ in September 2023. Data for this study was collected between March and May in 2019.

Sl. No.	**Scientific Name**	**Common Name**	**Local Name**	**Weight (kg)**	**IUCN Status / Population trend**
1	*Rusa unicolor*	Sambar	Manjang / Rusa	200	Vulnerable / Decreasing
2	*Muntiacus atherodes*	Bornean yellow muntjac	Kijang rimba	18	Near Threatened / Decreasing
3	*Muntiacus muntjak*	Southern red muntjac	Kijang bawas	24	Least Concern / Decreasing
4	*Sus barbatus*	Bearded pig	Babi hutan	130	Vulnerable / Decreasing
5	*Tragulus kanchil*	Lesser oriental mouse deer	Pelanduk	2.3	Least Concern / Unknown
6	*Tragulus napu*	Greater oriental mouse deer	Pelanduk	4.3	Least Concern / Decreasing
7	*Arctictis binturong*	Binturong	Binturong	13.1	Vulnerable / Decreasing
8	*Paguma larvata*	Masked palm civet	na	4	Least Concern / Decreasing
9	*Arctogalidia trivirgata*	Small-toothed palm civet	na	3.3	Least Concern / Decreasing
10	*Paradoxurus hermaphroditus*	Common palm civet	Munsang	2.5	Least Concern / Decreasing
11	*Viverra tangalunga*	Malay civet	Kuching batu	3.9	Least Concern / Stable
12	*Helarctos malayanus*	Sun bear	Beruang	42.5	Vulnerable / Decreasing
13	*Hystrix brachyura*	Malayan porcupine	Landak	8	Least Concern / Decreasing
14	*Hystrix crassispinis*	Thick-spined porcupine	Landak bulah	4.6	Least Concern / Stable
15	*Trichys fasciculata*	Long-tailed porcupine	Angkis	1.8	Least Concern / Stable
16	*Petaurista petaurista*	Red giant flying squirrel	Kubung	2	Least Concern / Decreasing
17	*Rheithrosciurus macrotis*	Tufted ground squirrel	Reribu	1.3	Vulnerable / Decreasing
18	*Ratufa affinis*	Pale giant squirrel	na	1.2	Near Threatened / Decreasing
19	*Callosciurus prevostii*	Prevost's squirrel	Kerabak	0.4	Least Concern / Decreasing
20	*Callosciurus sp.*	Small squirrel species	Tupai biasa	0.2	Least Concern / Stable

21	*Pongo pygmaeus*	Bornean orangutan	Orangutan	67.5	Critically Endangered / Decreasing
22	*Hylobates albibarbis*	Bornean white-bearded gibbon	Kelempiau	6	Endangered / Decreasing
23	*Macaca nemestrina*	Southern pig-tailed macaque	Berok	6.5	Endangered / Decreasing
24	*Macaca fascicularis*	Long-tailed macaque	Kera	5	Endangered / Decreasing
25	*Presbytis rubicunda*	Red langur	Kelasi	6.3	Vulnerable / Decreasing
26	*Pteropus vampyrus*	Large flying-fox	Keluang	0.9	Endangered / Decreasing
27	*Anorrhinus galeritus*	Bushy-crested hornbill	Burung ruwi/rui	1.2	Near Threatened / Decreasing
28	*Anthracoceros albirostris*	Oriental pied hornbill	Burung ayah	0.8	Least Concern / Stable
29	*Anthracoceros malayanus*	Black hornbill	Burung larak	1.1	Vulnerable / Decreasing
30	*Buceros rhinoceros*	Rhinoceros hornbill	Burung tingang	3	Vulnerable / Decreasing
31	*Rhinoplax vigil*	Helmeted hornbill	Penegung	2.9	Critically Endangered / Decreasing
32	*Rhabdotorrhinus corrugatus*	Wrinkled hornbill	Burung kukuk	1.6	Endangered / Decreasing
33	*Rhyticeros undulatus*	Wreathed hornbill	Burung kukuk	2.3	Vulnerable / Decreasing

Table C4.2. List of fruit-and seed-eating mammal and large bird species included in this study that could not be identified by respondents, along with the total number of respondents (of 25) who failed to recognize or distinguish between these species.

Group	**Common name**	**Scientific name**	**Number of respondents**
Civets	Binturong	*Arctictis binturong*	8
	Masked palm civet	*Paguma larvata*	8
	Small-toothed palm civet	*Arctogalidia trivirgata*	6
	Malay civet	*Viverra tangalunga*	5
Squirrels	Pale giant squirrel	*Ratufa affinis*	14
	Tufted ground squirrel	*Rheithrosciurus macrotis*	4
	Red giant flying squirrel	*Petaurista petaurista*	2
Porcupines	Thick-spined porcupine	*Hystrix crassispinis*	2
Hornbills	Wreathed hornbill	*Rhyticeros undulatus*	20
	Wrinkled hornbill	*Rhabdotorrhinus corrugatus*	17
	Black hornbill	*Anthracoceros malayanus*	9
	Helmeted hornbill	*Rhinoplax vigil*	6
	Oriental pied hornbill	*Anthracoceros albirostris*	3
	Bushy-crested hornbill	*Anorrhinus galeritus*	2
	Rhinoceros hornbill	*Buceros rhinoceros*	2

Table C4.3. Use of animal parts in traditional medicines, displaying the frequency (freq.) of respondents reporting the use of animal parts, the medicinal value attributed to these parts, and the methods of medicine preparation. The average sale price is listed in Indonesian rupiah (1 USD = 14525.1 IDR in May 2019). The 'User' column indicates the ethnic community utilizing the animal parts in medicine, with 'M' denoting Melayu, 'D' representing Dayak, 'C' for Chinese, and 'NM' for non-Muslims (when a specific non-Muslim community wasn't reported).

Common name	Scientific name	Part used in Bahasa (English)	Medicinal value (freq.)	Method (freq.)	Freq. (part used)	Avg. sale price	User
Sun bear	*Helarctos malayanus*	empedu (gallbladder)	internal injuries from falls and other causes (14); accidental injuries from falls and other causes (9); hematemesis (4); lung disease (3); migraine (2); typhus (2); malaria (2); don't know (2); postpartum acute phase (1); improve stamina (1)	sewn or as is, dried or fresh, at times pierced, soaked in water (hot or room temperature), and the water is consumed (16); don't know (7); cleaned, contents discarded, boiled and the water is consumed (2)	25	660000/ part (n=5)	M, D
		kulit (skin)	accidental injuries from falls and other causes (5); internal injuries from falls and other causes (5); asthenia (2); don't know (1)	dried, powdered, mixed in water, and the water is consumed (6); don't know (3); boiled in water, and the water is consumed (2); dried and laid out, and the injured person sleeps on it to recover (2)	13	NA	M
		hati (liver)	don't know	don't know	1	NA	M

Malayan porcupine	*Hystrix brachyura*	geliga (bezoar stone)	don't know (10); rheumatism (2); strokes (2); internal injuries (2); urinary retention (1); uncomplicated / smooth labor (1)	don't know (10); soaked in water and the water is consumed (4); dried, boiled, and the water is consumed (2)	16	340000/g (n=2)	M, C
		ekor (tail)	high fever (particularly children) (2); chicken pox (2); urinary retention (1); veisalgia (1); don't know (1)	boiled or soaked in water, and the water is consumed (4); don't know (2)	6	NA	M
		empedu (gall bladder)	fever (2); cough (2); accidental injuries (2); asthenia (1); internal injuries from falling (1); lung disease (1)	dried, at times pierced, soaked in hot water, and the water is consumed (4)	4	NA	M
		bulu (quill)	fever in children (2)	soaked in water, and the water is consumed (2)	2	NA	M
		gigi (teeth)	urinary retention; veisalgia	soaked in water and the water is consumed	1	NA	M
Thick-spined porcupine	*Hystrix crassispinis*	geliga (bezoar stone)	unknown (7); rheumatism (2); Strokes (2); Internal injuries (2)	unknown (6); dried or fresh, boiled or soaked in water, and the water is consumed (5)	11	350000/g (n=1)	M, C
		ekor (tail)	high fever (particularly children) (2); chicken pox (2); urinary retention (1); veisalgia (1); unknown (1)	boiled or soaked in water, and the water is consumed (4); unknown (2)	6	NA	M

		empedu (gallbladder)	fever (2); cough (2); accidental injuries (2); internal injuries from falling (1); asthenia (1)	dried or fresh, at times pierced, soaked in hot water, and the water is consumed (4)	4	NA	M
		gigi (teeth)	urinary retention; veisalgia	soaked in water and the water is consumed	1	NA	M
Long-tailed porcupine	*Trichys fasciculata*	geliga (bezoar stone)	don't know (5)	don't know (5)	5	500000/g (n=1)	M, C
		empedu (gallbladder)	fever (2); cough (2); accidental injuries (2)	dried, soaked in hot water and the water is consumed (2)	2	NA	M
		ekor (tail)	don't know	don't know	1	NA	M
		daging (meat)	asthenia; fatigue	cooked and eaten	1	NA	M
Large flying- fox	*Pteropus vampyrus*	hati (liver)	asthma (5); cough (2); asthenia (1); internal injuries from falling in children (1)	cleaned, cooked, and eaten (6)	6	NA	M, D
		empedu (gallbladder)	asthma (2); pruritus (1); allergies (1); internal injuries from falling in children (1); don't know (1)	dried or fresh, at times pierced, soaked in hot or normal water, and the water is consumed (2); cleaned, cooked, and eaten (2); don't know (1)	5	NA	M, D
		daging (meat)	asthma (2); internal injuries from falling (1)	cleaned, cooked, and eaten (3)	3	300000/animal (n=1)	M, D

Greater oriental mouse deer	*Tragulus napu*	selusuh (unknown)	uncomplicated / smooth labor (4)	soaked in water and the water is consumed (3); dried and mixed with cooking oil and massaged on to the belly (2); dried and then swallowed (1); dried and mixed with food and consumed (1)	4	NA	M
		empedu (gallbladder)	don’t know	don’t know	1	NA	M
Lesser oriental mouse deer	*Tragulus kanchil*	selusuh (unknown)	uncomplicated / smooth labor (4)	soaked in water and the water is consumed (3); dried and mixed with cooking oil and massaged on to the belly (2); dried and then swallowed (1); dried and mixed with food and consumed (1)	4	NA	M
		empedu (gallbladder)	don’t know	don’t know	1	NA	M
Red langur	*Presbytis rubicunda*	geliga (bezoar stone)	don’t know (3)	don’t know (3)	3	4500000/piece (n=2) 350000/g (n=1)	NM
		empedu (gallbladder)	internal injuries (2); asthenia (2); migraine (2); poor vision (2)	dried, pierced, soaked in water, and the water is consumed (2)	2	NA	M
Bornean orangutan	*Pongo pygmaeus*	empedu (gallbladder)	asthenia; asthma; internal injuries	don’t know	1	1750000/part (n=1)	C
Bornean white-	*Hylobates albibarbis*	empedu (gallbladder)	asthenia; asthma;	don’t know	1	1750000/part (n=1)	C

bearded gibbon			internal injuries				
Small squirrel species	*Callosciurus sp.*	daging (meat)	poor vision (2); improve stamina (2)	cooked and eaten (2)	2	NA	D, C
Pale giant squirrel	*Ratufa affinis*	daging (meat)	diabetes (2); lung disease (2)	don’t know (2)	2	NA	D, C
		empedu (gallbladder)	internal injuries	soaked in water and the water is consumed	1	NA	D, C
Sunda pangolin	*Manis javanica*	daging (meat)	don’t know	don’t know	1	NA	NM
Rhinoceros hornbill	*Buceros rhinoceros*	paruh (beak)	asthenia (2); rheumatism (2); healthy body (1); feel rejuvenated (1)	the beak is boiled until the red part separates from the white, and the red part is dried & stored, and when required it is boiled for a short period of time in water, and the water is consumed (3)	3	NA	M
Borneo python	*Python breitensteini*	lemak (fat)	fractures (2)	like oil massaged on to the skin (2)	2	NA	NM
Cobra sp.	*Naja sp.*	don’t know	don’t know	don’t know	1	500000/ animal (n=1)	C

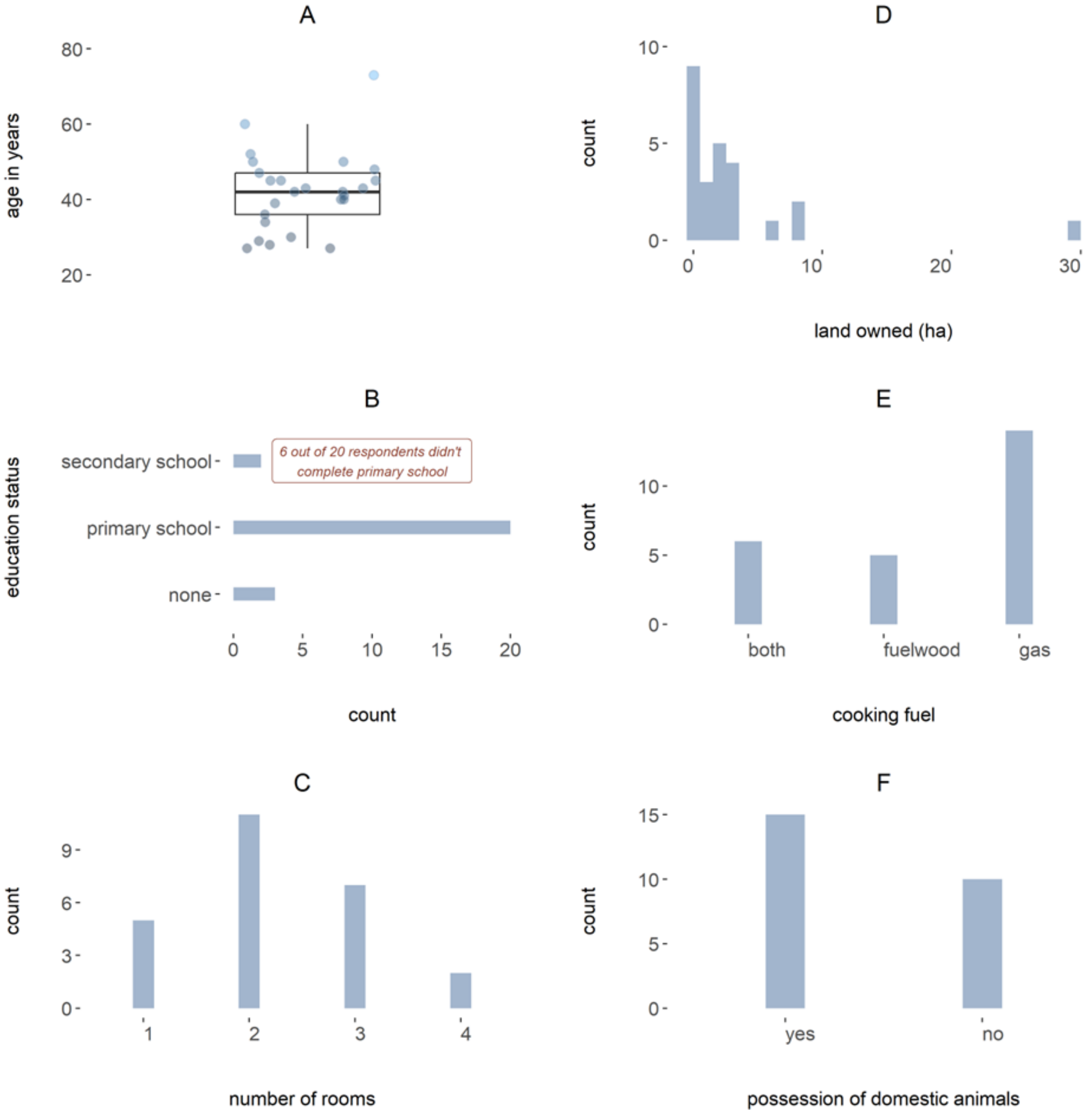
Table C4.4. Comparison of ordered logit models used to evaluate the influence of AGE - age of respondents (continuous), INA - monthly household income (continuous), AMU - amount of land owned (continuous), POD - possession of domestic animals (binary), HLH - number of years they have been hunting (discrete), HOE - how often wild meat is consumed (ordered categorical), HOS - how often wild meat is sold (ordered categorical), DMC - how often domestic meat is consumed (ordered categorical), and PWD - preference of wild or domestic meat (binary), on HOH - how often a respondent hunted (ordered categorical). The table includes key model comparison metrics such as log-likelihood (logLik), corrected Akaike Information Criterion (AICc), delta (the difference in AICc between the model and the best model), and weight, representing the Akaike weight, signifying the level of support or evidence of a model being the most parsimonious among the candidate model set.

model	**df**	**logLik**	**AICc**	**delta**	**weight**
HOH ~ HOE	5	-21.23	55.63	0.00	0.35
HOH ~ AGE + HOE	6	-20.30	57.27	1.64	0.16
HOH ~ HOE + PWD	6	-20.87	58.40	2.77	0.09
HOH ~ POD + HOE	6	-20.92	58.52	2.89	0.08
HOH ~ HLH + HOE	6	-20.96	58.59	2.97	0.08
HOH ~ INA + HOE	6	-21.03	58.73	3.10	0.08
HOH ~ AMU + HOE	6	-21.14	58.96	3.33	0.07
HOH ~ 1	3	-27.43	62.00	6.38	0.01
HOH ~ AGE	4	-26.19	62.37	6.74	0.01
HOH ~ AGE + POD	5	-24.93	63.03	7.40	0.01
HOH ~ POD	4	-26.82	63.65	8.02	0.01
HOH ~ AMU	4	-27.06	64.11	8.49	0.01
HOH ~ HLH	4	-27.08	64.15	8.52	0.00
HOH ~ HOE + HOS	8	-19.60	64.20	8.57	0.00
HOH ~ AGE + AMU	5	-25.63	64.41	8.78	0.00
HOH ~ PWD	4	-27.37	64.75	9.12	0.00
HOH ~ INA	4	-27.41	64.83	9.20	0.00
HOH ~ AMU + POD	5	-25.90	64.95	9.32	0.00
HOH ~ AGE + HLH	5	-26.10	65.35	9.73	0.00
HOH ~ AGE + INA	5	-26.16	65.49	9.86	0.00
HOH ~ AGE + PWD	5	-26.18	65.52	9.89	0.00
HOH ~ POD + HLH	5	-26.45	66.06	10.43	0.00
HOH ~ AMU + HLH	5	-26.56	66.28	10.65	0.00
HOH ~ POD + PWD	5	-26.72	66.59	10.96	0.00
HOH ~ HOE + DMC	8	-20.87	66.73	11.11	0.00
HOH ~ INA + POD	5	-26.79	66.74	11.11	0.00
HOH ~ INA + AMU	5	-26.98	67.11	11.48	0.00
HOH ~ AMU + PWD	5	-27.04	67.24	11.62	0.00
HOH ~ INA + HLH	5	-27.05	67.26	11.64	0.00
HOH ~ HLH + PWD	5	-27.06	67.28	11.65	0.00
HOH ~ INA + PWD	5	-27.33	67.82	12.19	0.00

HOH ~ AGE + DMC	7	-23.97	68.52	12.89	0.00
HOH ~ DMC	6	-26.07	68.80	13.18	0.00
HOH ~ HLH + DMC	7	-24.77	70.13	14.50	0.00
HOH ~ HOS	6	-27.02	70.70	15.07	0.00
HOH ~ POD + DMC	7	-25.45	71.49	15.86	0.00
HOH ~ AGE + HOS	7	-25.79	72.16	16.53	0.00
HOH ~ INA + DMC	7	-25.87	72.32	16.70	0.00
HOH ~ AMU + DMC	7	-25.96	72.50	16.88	0.00
HOH ~ POD + HOS	7	-25.98	72.54	16.92	0.00
HOH ~ DMC + PWD	7	-25.99	72.56	16.93	0.00
HOH ~ HLH + HOS	7	-26.71	74.01	18.38	0.00
HOH ~ AMU + HOS	7	-26.73	74.04	18.42	0.00
HOH ~ HOS + PWD	7	-26.90	74.39	18.76	0.00
HOH ~ INA + HOS	7	-27.02	74.62	18.99	0.00
HOH ~ HOS + DMC	9	-25.52	81.05	25.42	0.00

Table C4.5. Conservation status of focal animal species as perceived by respondents. Respondents were asked to reflect on the population status of animals, comparing it to 30 years ago (or an appropriate time frame for younger respondents). Values represent the percentage of 25 respondents who reported a specific conservation status for each species.

Common name of hunted focal species	**% of 25 respondents**				
	complete extirpation or extreme reduction	**moderate reduction**	**no change**	**moderate increase**	**extreme increase**
Sambar	100	0	0	0	0
Bornean Orangutan	60	8	28	4	0
Greater oriental mouse deer	56	20	24	0	0
Lesser oriental mouse deer	56	20	24	0	0
Southern red muntjac	40	32	28	0	0
Bornean yellow muntjac	36	32	32	0	0
Sun bear	36	20	36	0	4
Helmeted hornbill	28	20	28	0	0
Red langur	28	8	60	0	4
Red giant flying squirrel	24	0	64	4	0
Long-tailed porcupine	20	16	60	0	4
Malayan porcupine	16	56	28	0	0
Bearded pig	12	12	56	8	12
Thick-spined porcupine	12	28	48	4	0
Bushy-crested hornbill	12	20	60	0	0
Pale giant squirrel	12	0	32	0	0
Bornean white- bearded gibbon	12	32	52	0	4
Malay civet	8	0	64	4	0
Rhinoceros hornbill	8	32	44	8	0
Wrinkled hornbill	8	0	32	0	0
Common palm civet	4	16	64	8	0
Oriental pied hornbill	4	12	64	8	0
Tufted ground squirrel	4	4	76	0	0
Black hornbill	0	8	48	8	0
Binturong	0	0	68	0	0
Small-toothed palm civet	0	16	52	0	0
Large flying-fox	0	4	72	0	24
Long-tailed macaque	0	0	48	8	44
Masked palm civet	0	12	56	0	0
Southern pig-tailed macaque	0	8	60	4	28
Prevost's squirrel	0	16	84	0	0
Small squirrel species	0	0	84	4	12
Wreathed hornbill	0	0	20	0	0



6 out of 20 respondents didn't complete primary school

Figure C4.1. Profile of hunters recruited into this study. Panel A displays the age of respondents, B presents the education level of respondents, C indicates the number of rooms in respondents' homes, D represents the amount of land owned in hectares by respondents, E shows whether respondents use fuelwood, gas, or both in their homes, and F depicts how many respondents own domestic animals.

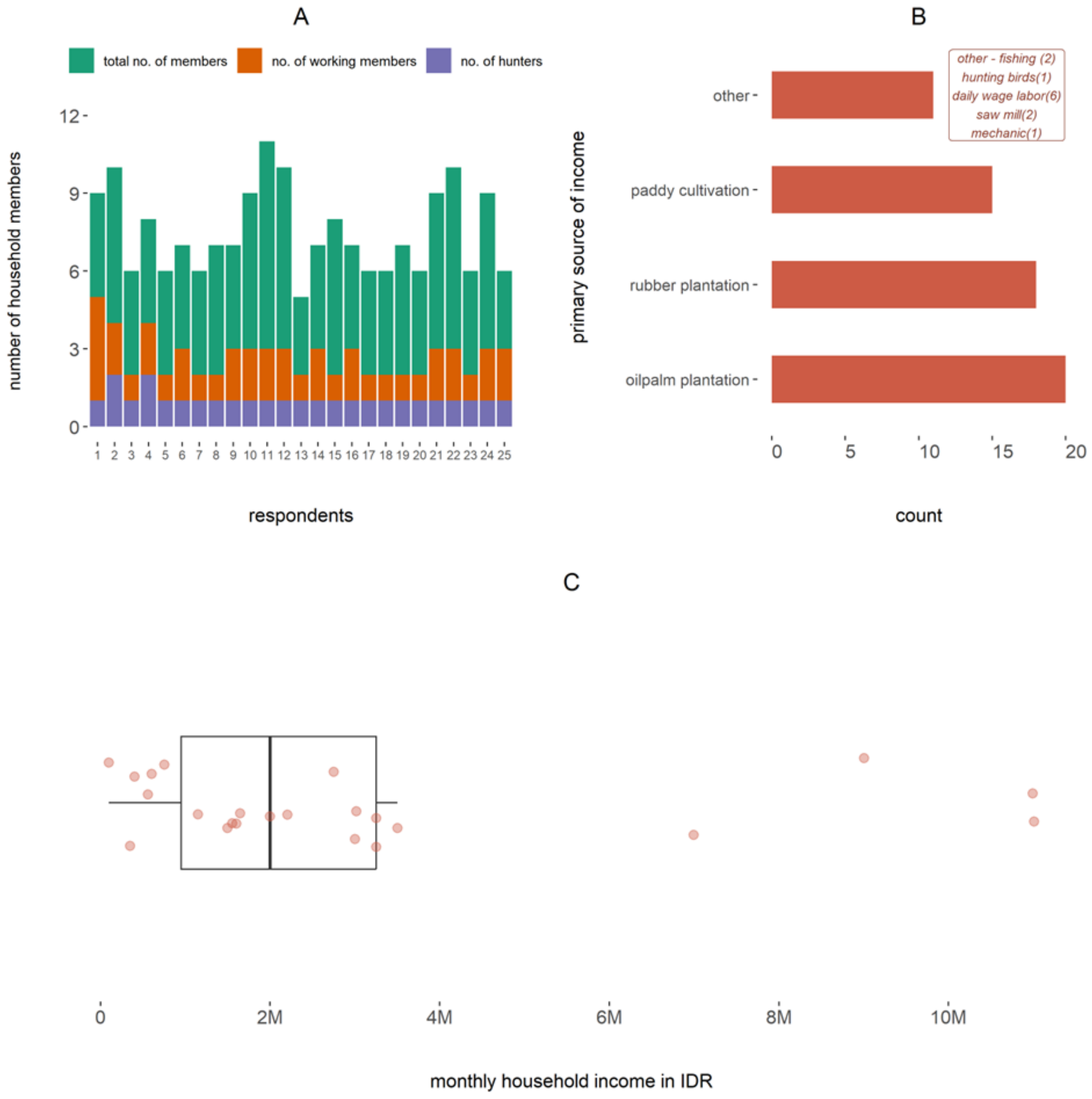


Figure C4.2. Profile of hunters recruited into this study. Panel A displays the number of household members, including working members and the number of hunters within each respondent's household. Panel B presents the primary sources of income listed by respondents. Panel C includes a box and whisker plot illustrating the monthly household income reported in Indonesian rupiah (1 USD = 14525.1 IDR in May 2019).

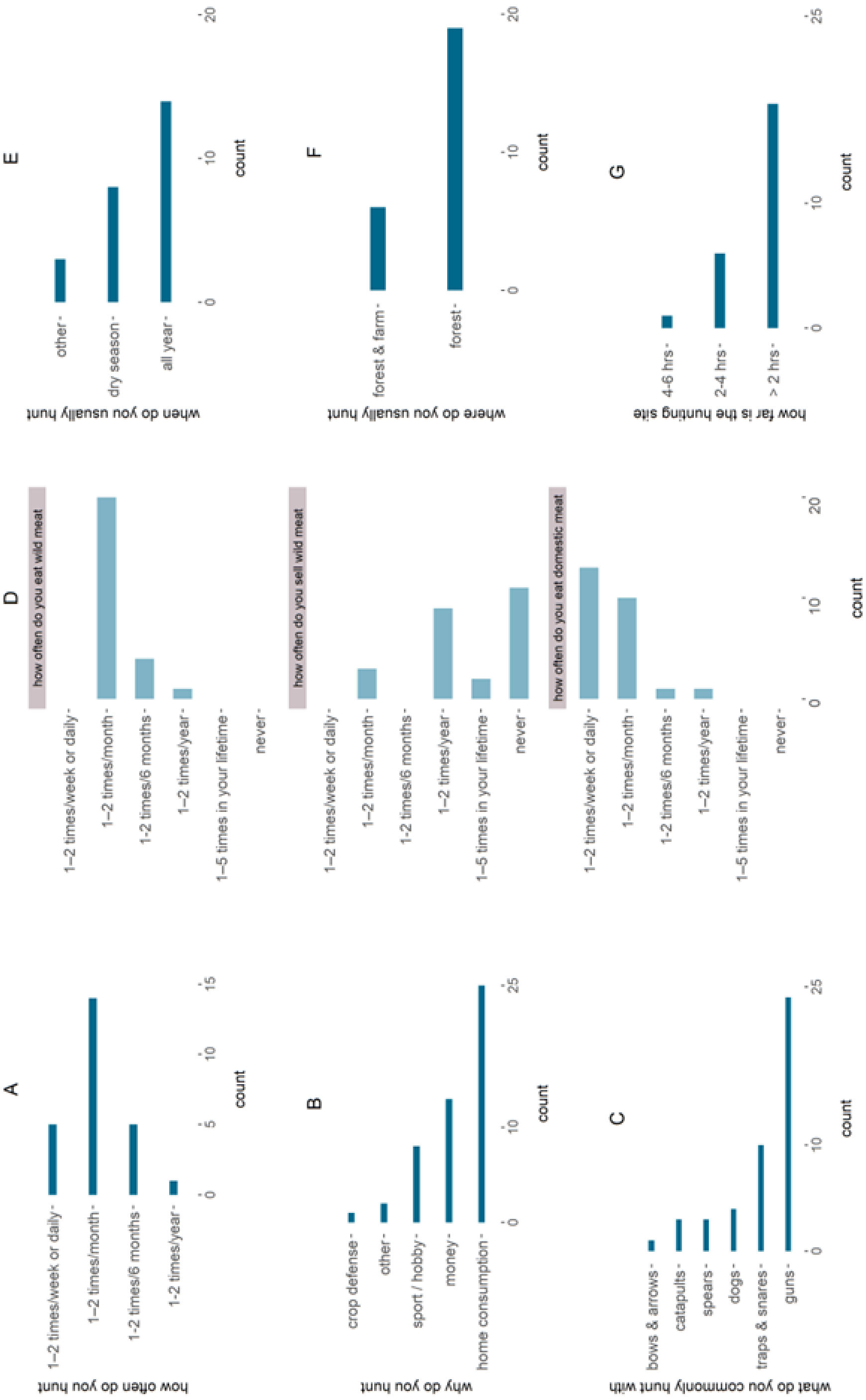


Figure C4.3. Current hunting practices. Panel A shows the frequencies of hunting, panel B presents hunting motivations, panel C displays the preferred method of hunting, panel D illustrates the frequency of meat consumption and sale, panel E indicates the hunting season, and panels F and G depict locations of hunting sites. The heights of the bars represent the number of respondents.

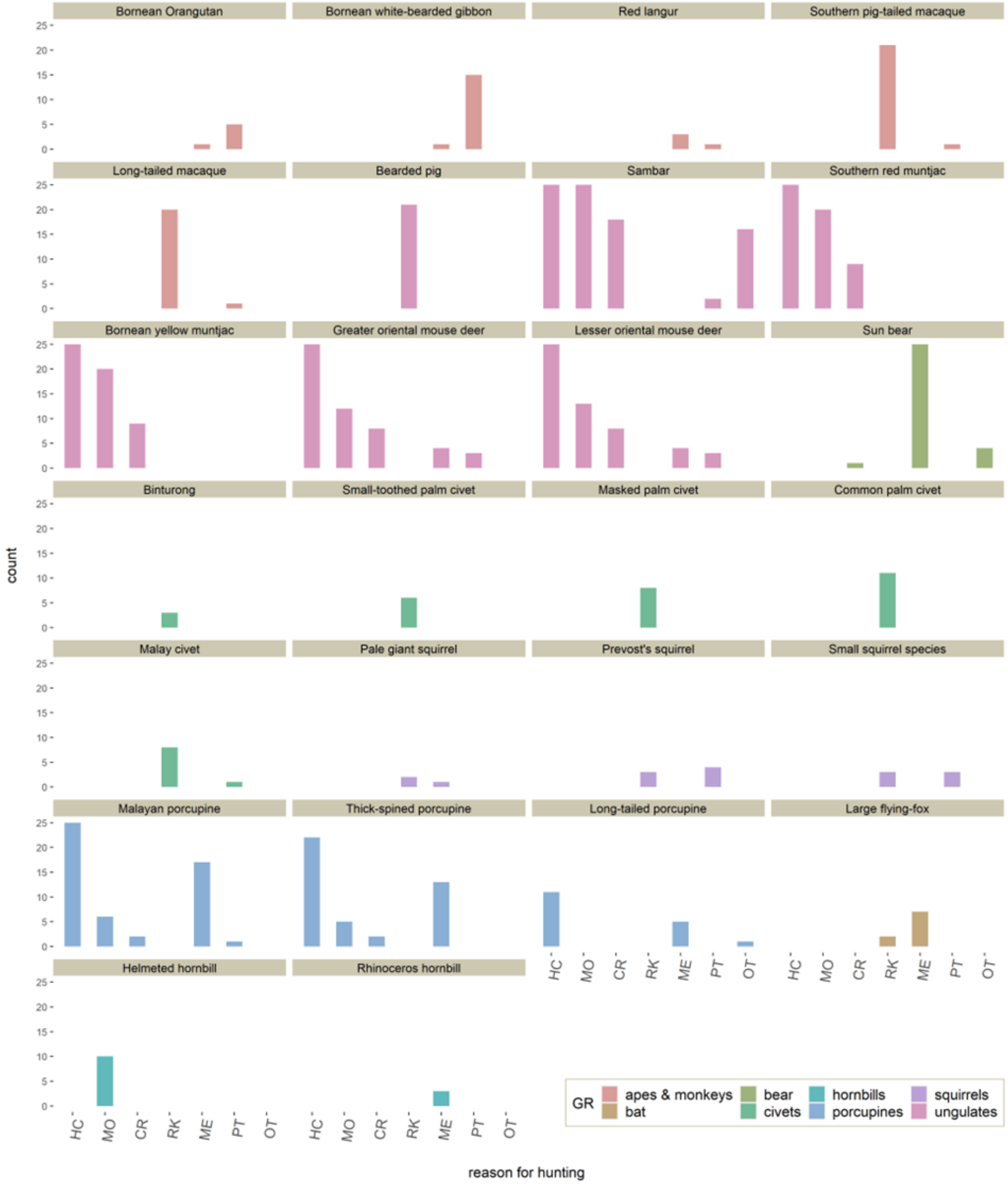


Figure C4.4. Motivations for hunting each of the 26 hunted focal species, with each species represented separately in individual panels. The bar heights indicate the number of respondents who reported specific motivations for hunting each species. On the x-axis, motivations for hunting are categorized as follows: 'HC' for consumption at home, 'MO' for monetary gain, 'CR' for cultural or religious purposes, 'RK' for retaliation due to crop damage or livestock predation, 'ME' for use in traditional medicines, 'PT' for capturing live animals for pet keeping, and 'OT' for other reasons.

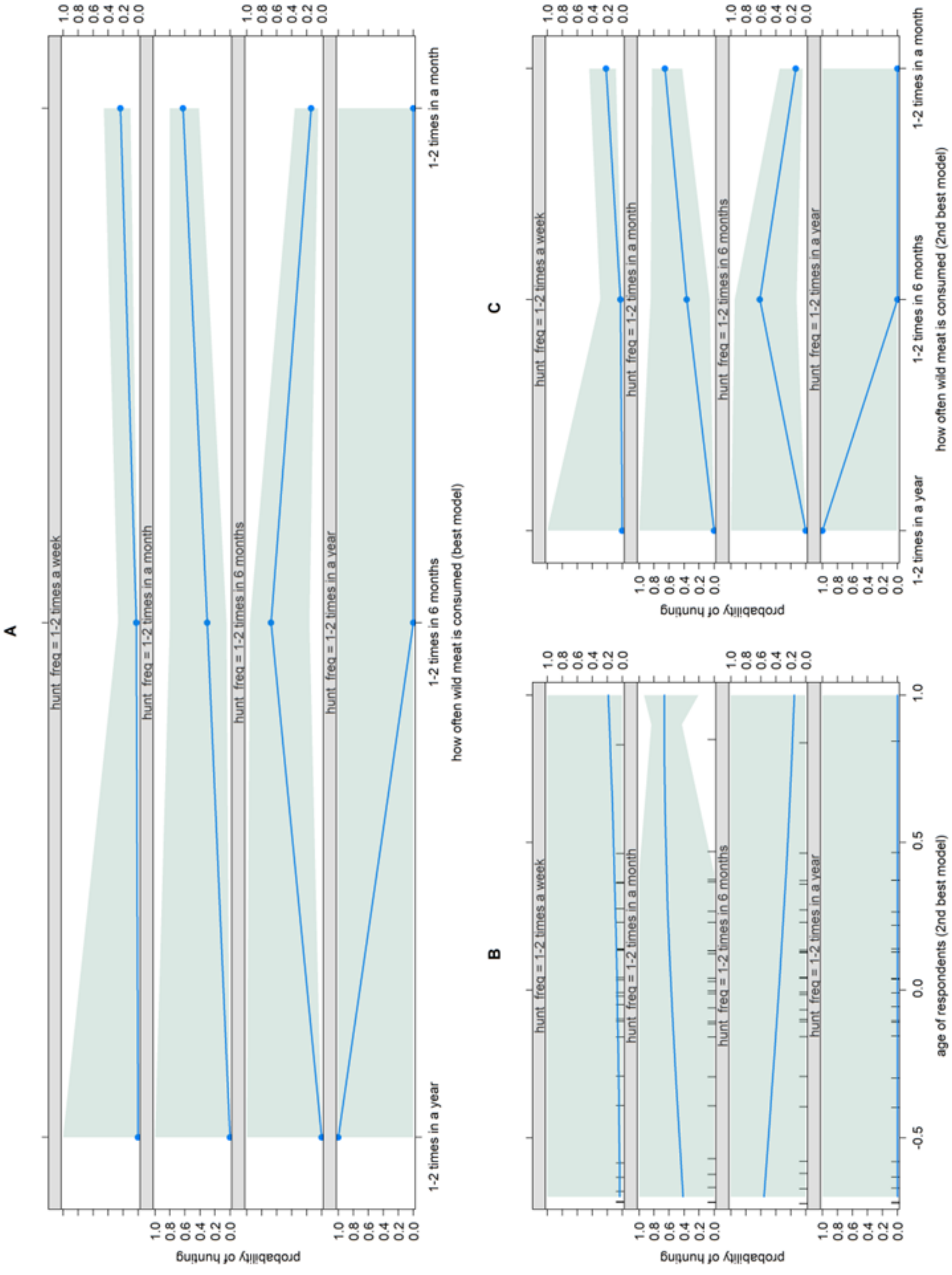


Figure C4.5. Model coefficients from the top two ordered logit models assessing the probability of hunting frequency. The best model examines hunting frequency as a function of wild meat consumption frequency, while the second-best model incorporates both wild meat consumption frequency and the age of respondents as predictors. Panel A illustrates the probability of hunting frequency (categorical variable) relative to the frequency of wild meat consumption (categorical variable). Panel B displays the probability of hunting frequency in relation to the age of respondents (continuous variable), one of the two predictors in the second-best model. Panel C illustrates the probability of hunting frequency in relation to the frequency of wild meat consumption, the other predictor in the second-best model.