

## Elephant frugivory and wild boar seed predation of *Irvingia malayana*, a large-fruited tree, in a rainforest of Peninsular Malaysia

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

**Key words.** Belum-Temengor, camera trap, megafauna, megafaunal-dispersal syndrome, plant-animal interactions, seed dispersal

### INTRODUCTION

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

While small fruits and large soft fruits with multiple small seeds have a larger assemblage of seed dispersers to depend on, large-fruited and large-seeded fleshy fruits are restricted to fewer dispersers, mostly large-bodied animals with a larger gape size (Corlett, 1998; Chen & Moles, 2015). Megafaunal syndrome fruits are fruits either of 4–10 cm in diameter with one to five large seeds, or fruits greater than 10 cm in diameter with multiple small seeds (Guimarães et al., 2008). In the Anthropocene, large-seeded plant species face a big challenge in sustaining their recruitment ability in increasingly fragmented and defaunated landscapes (Cramer et al., 2007; McConkey et al., 2011). The extinction of megafauna (often defined as animals more than 100 pounds or 44.5 kg; Martin, 1984) from South America around 10–15 Kyr BP has been linked to great losses in seed dispersal processes (Janzen & Martin, 1982; Guimarães et al., 2008; Doughty et al., 2016).

Little is known about the ecology of megafaunal-syndrome plants in tropical Asia. In Malaysia, there are large-fruited and large-seeded plant species (included but not restricted to megafaunal-syndrome plants) that may rely on large-bodied animals for their dispersal. Defaunation and megafauna loss in the region, however, is ongoing at a dramatic pace (Sodhi et al., 2004; Corlett, 2007) and the remaining large mammals might be inadequate to replace the largest seed dispersers. For example, Malayan tapirs (*Tapirus indicus*) disperse small-seeded plants but are seed predators for large-seeded ones (Campos-Arceiz et al., 2012), wild bovids disperse seeds over shorter distances and their

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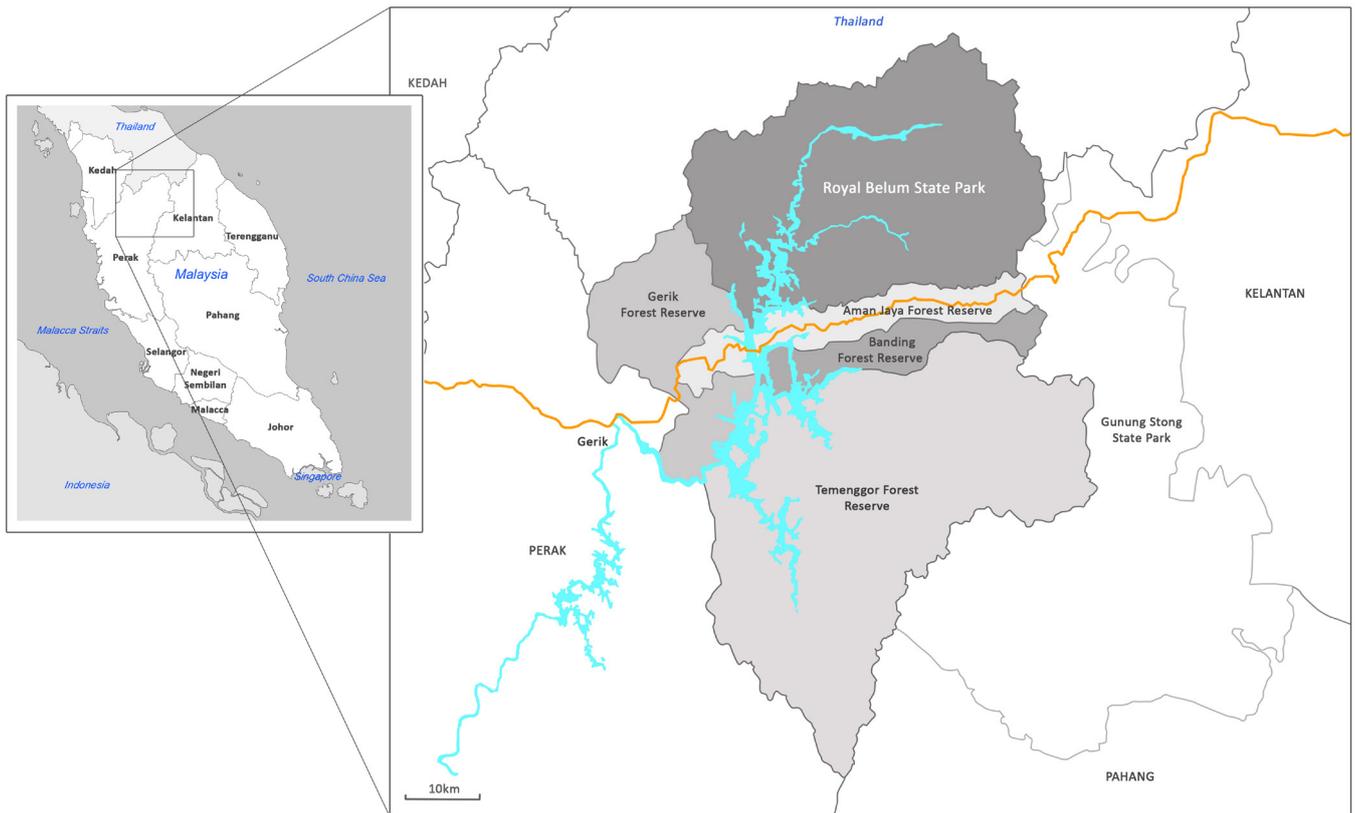


Fig. 1. Map of Belum Temenggor Forest Complex (BTFC), in Perak, northern Peninsular Malaysia.

digestive systems reduce seed germinability (Sekar et al., 2015), and gibbons are unable to swallow very large seeds (McConkey, 2000; McConkey et al., 2015). After the loss of two rhinoceros species (*Dicerorhinus sumatrensis* and *Rhinoceros sondaicus*; see Havmøller et al., 2015), Asian elephants (*Elephas maximus*) might be one of the few, sometimes the main, effective long-distance dispersers for large-seeded plants, providing high seed loads, long-distance dispersal, and reliable germination viability (Kitamura et al., 2007; Samansiri & Weerakoon, 2007; Campos-Arceiz et al., 2008; Campos-Arceiz & Blake, 2011). The impact of forest elephants on tropical tree diversity, however, remains unclear and has been questioned (see Hawthorne & Parren, 2000; and Blake et al., 2009, for contrasting opinions).

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

seed predation of fleshy fruits is mainly attributed to a few taxonomic groups such as tapirs, pigs, deer, squirrels, rats, and mice (Corlett, 1998; Campos-Arceiz et al., 2012). Little is known about their interaction with large-fruited plants.

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

## MATERIAL AND METHODS

**Study site.** This study was conducted in Belum-Temenggor Forest Complex (BTFC; 5°30'N, 101°20'E), in northern Peninsular Malaysia (Fig. 1). BTFC occupies an area of 3,546 km<sup>2</sup> including the Royal Belum State Park (1,175 km<sup>2</sup>; gazetted in 2007), four permanent forest reserves (Temenggor, Gerik, Banding, and Aman Jaya), and the man-made Temenggor lake (Lim, 2010; Mohd Hasmadi et al., 2013; Hanis et al., 2014). BTFC is listed as an Environmentally Sensitive Area under Malaysia's National Physical Plan and contains a crucial wildlife corridor under the Federal Government's Central Forest Spine Masterplan to promote connectivity among major forest patches in Peninsular Malaysia (Government of Malaysia et al., 2014). The East-West Highway bisects the forest complex, dividing it into two large blocks (Fig. 1). Logging is permitted and ongoing inside the permanent forest reserves.

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

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

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

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

Hamilton & Galdikas, 1994; Kitamura et al., 2002). In the studies by Kitamura et al. (2002, 2007), elephants were the only seed dispersers.

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

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

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

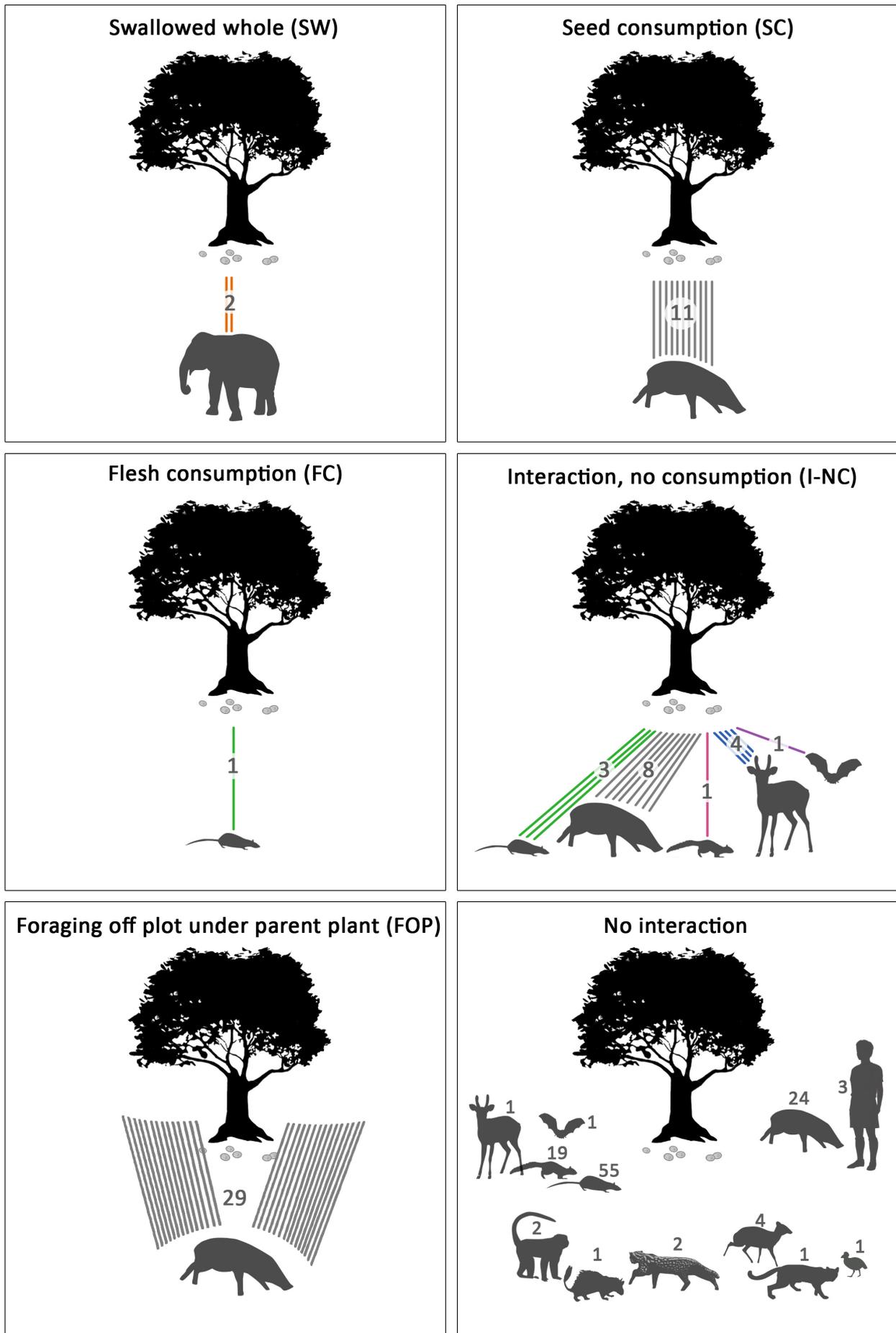


Fig. 2. Type and frequency of interactions between vertebrates and *Irvingia malayana* trees, fruits, and seeds; each line represents one visit with the interaction type observed.

germination curve declined towards a horizontal asymptote. The seeds that had not germinated after 14 weeks were cut open and examined to check if they were alive (still yellow and healthy) or dead (brown and infected).

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

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

## RESULTS

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

Two of our camera setups failed, which resulted in a final sampling effort of eight bouts (three cameras  $\times$  two bouts and two cameras  $\times$  one bout) and a total of 86 camera trap nights. A total of 391 videos representing 145 independent

visits by 12 vertebrate groups (11 mammal and one bird species; Table 1), excluding humans, were recorded. Three animal groups – rats, wild boars, and squirrels – accounted for 84.1% of all the visits (n=122). Three species – Asian golden cat (*Catopuma temminckii*), brush-tailed porcupine (*Atherurus macrourus*), and the crested partridge (*Rollulus rouloul*) were recorded just once. Of all the animal groups captured, only three – rats, wild boars, and elephants – consumed at least some part of the bait fruits; three groups – barking deer, squirrels, and bats – interacted with the fruits without consumption; while the others did not interact with the fruits (Table 1; Fig. 2).

Rats were the most commonly captured animal on the camera traps, representing 40.7% (n=59) of the 145 independent visits. They consumed fruit flesh in one visit only (i.e., 1.7% of their visits) and interacted without consumption in three other visits (5.1%; Table 1). Wild boars were the second most frequently captured animals, in 29.7% (n=43) of the 145 independent visits. Wild boars predated on *I. malayana* seeds in 25.6% (n=11) of their visits, which they did by crushing the hard endocarp, with audible cracking sounds heard through the recordings (Fig. 3a, 3b). In 18.6% (n=8) of their visits, wild boars interacted with the fruits without consumption. In 67.4% (n=29) of their visits, they showed no interaction with the fruits but were observed foraging off-plot (i.e., under the same tree but far from the camera trap main field of vision). Wild boars visited four of the five focal trees. Elephants were recorded just twice (1.4% of all the 145 visits; at two different trees). In both visits, elephants swallowed fruits whole (Fig. 3c, 3d). Barking deer were recorded sniffing but did not consume any fruits in 80.0% of their visits (n=4); in the remaining 20% (n=1), barking deer had no interaction with the fruits. Of the two bat visits recorded, one captured a bat flying close to the fruits. Squirrels were frequently recorded, but they sniffed the bait fruits in only one case (Table 1).

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

Elephants and wild boars also differed in the timing of their fruit consumption. In both cases in which elephants were observed consuming bait fruits, the bait fruits were less than two days old – in one case, the fruits had been added (by our team) the day before; in the other, elephants consumed fruits that had naturally fallen from the tree about six hours before their visit. Elephants seemed to pick these fresh fruits while ignoring the old ones (Fig. 4a). Wild boars, on the other hand, seemed to prefer older fruits; whereby 78.7% of the fruits they consumed were eight days or older (Fig. 4a, 4b); average day of consumption by wild boar was  $8.2 \pm 2.1$  days. In the first week since the bait fruits were set, wild boars consumed seeds in three out of 21 visits, sniffed and ignored bait fruits in seven visits, and were recorded foraging off-plot in 17 visits (Fig. 4b).

Table 1. Vertebrate visits and their interactions with *Irvingia malayana* fruits. NA = unidentified species; Visits = total number of independent visits; INC = interaction without consumption; FC = flesh consumption; SW = whole fruit swallowed; SC: seed consumption; FOP: foraging off-plot; NI = no interaction.

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

Table 2. Results of germination test of *I. malayana* seeds using three different treatments. Treatments: D+IS = elephant-ingested seeds planted in dung; D+S = depulped control seeds planted in dung; S = depulped control seeds planted in forest soil. CV= coefficient of variation; germ. = germination.

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

Germinability was highest in control seeds planted in dung (96.7%), followed by control seeds in soil (81.6%), and ingested seeds (75.0%; Table 2 and Fig. 5). Germination variability was high in all treatments (above 20%). Ingested seeds exhibited higher uncertainty (1.7) and lower synchronisation (0.6), compared to control seeds in dung (1.6 and 0.4, respectively) and in forest soil (1.0 and 0.6, respectively; Table 2). Ingested seeds exhibited a steeper germination curve compared to non-ingested seeds (Fig. 5). After 14 weeks, all the non-germinated seeds were found to be infected with fungus and dead.

## DISCUSSION

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

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

The results of our small-scale germination test show that *I. malayana* seeds dispersed by elephants are generally viable (75.0%), although this percentage is lower than that of the manually depulped seeds. Having a hard endocarp in a fruit size easy for elephants to swallow, the seeds of *I. malayana* swallowed by elephants were unlikely to be damaged by chewing or digestion (Campos-Arceiz & Blake, 2011). Asian elephants provide effective long-distance dispersal



Fig. 3. (a), Wild boars (*Sus scrofa*) consuming *Irvingia malayana* seeds; (b), crushed endocarps after being eaten by wild boars; (c), Asian elephants (*Elephas maximus*) consuming *I. malayana* fruits; (d), *I. malayana* seedling found in elephants' dung in the field.

while removing seeds from density competition, pathogens, and seed predation under parent plant (Augsburger, 1984; Campos-Arceiz & Blake, 2011; Sekar et al., 2015); they are thus likely to play a key role in the long-term survival and genetic diversity of large-fruited and large-seeded plants, such as *Irvingia malayana*.

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

at the beginning of the 21<sup>st</sup> century. Defaunation might, therefore, have reduced the number of effective dispersers of *I. malayana*, and the frequency of their visit in BTFC.

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

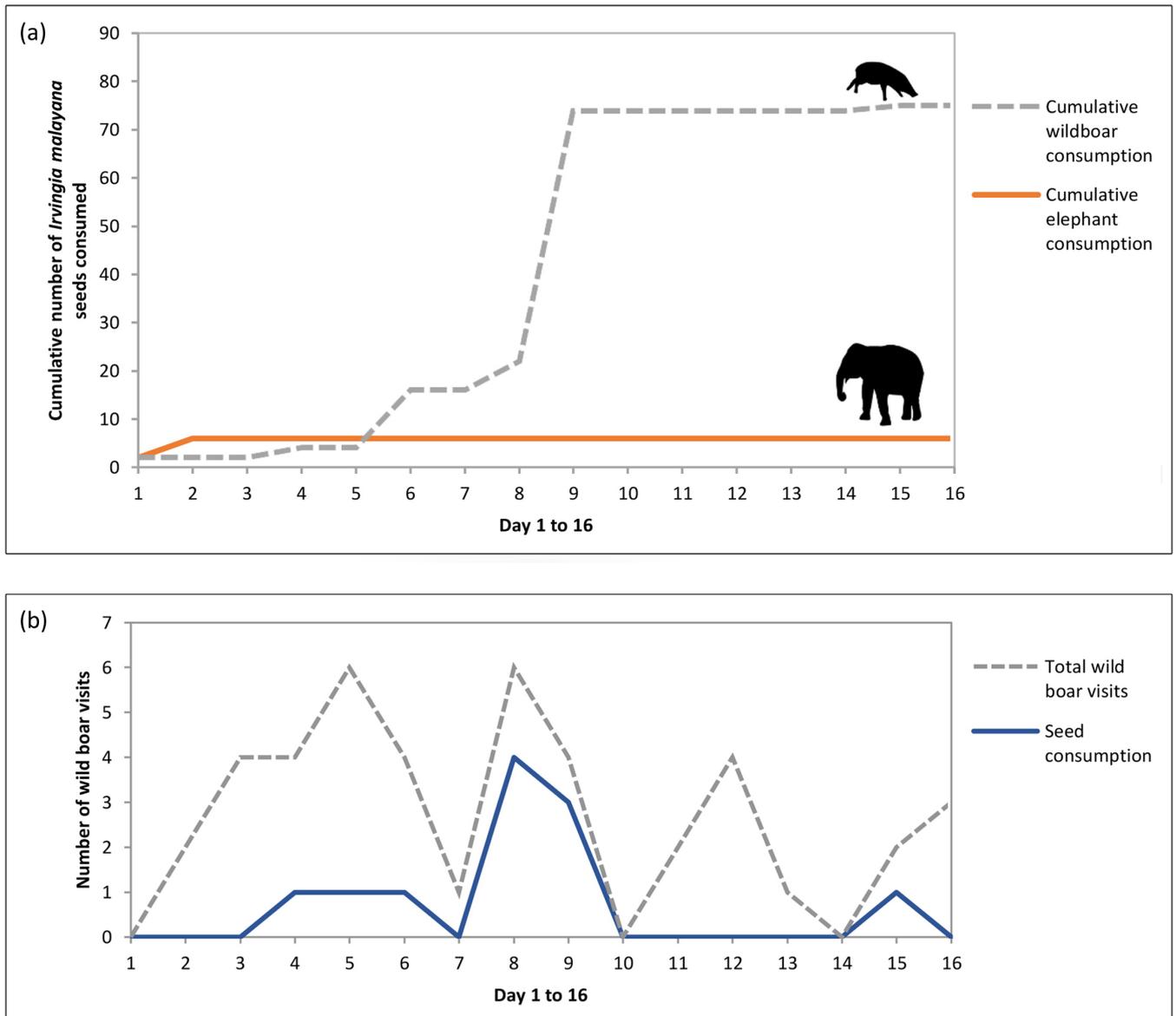


Fig. 4. (a), Temporal differences in the consumption of *Irvingia malayana* fruits and seeds by wild boars (*Sus scrofa*) and Asian elephants (*Elephas maximus*). Note that elephants only consumed fresh fruits (< 2 days old) while wild boars consumed seeds from old fruits (generally > 5 days old); (b), Temporal distribution of all wild boar visits and their seed consumption.

primates are thus unlikely to be effective dispersers of *I. malayana* seeds to safe sites for successful germination (Schupp et al., 2010; McConkey et al., 2015).

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

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

provide some secondary seed dispersal to *I. malayana* seeds, although this was not recorded in our sample.

Wild boars acted as seed predators, destroying 24.4% (n=76) of the bait seeds, which they crushed despite *I. malayana* having hard endocarps. Wild boars seemed to have waited for the pulp of *I. malayana* fruits to turn soft before consuming them (Fig. 4). In Central Indonesian Borneo, Hamilton & Galdikas (1994) found orang utans to predate on *Irvingia malayana* – interestingly, *Irvingia malayana* seeds were a predominant part of orang utans diet in a period of three months (October to December 1980), while the orang utans had ignored them in previous fruiting years (Hamilton & Galdikas, 1994).

We observed what could be a temporal resource partitioning between a megafaunal syndrome plant’s frugivore and a seed predator. Barnea et al. (1993) suggested that secondary compounds in pulp can deter about consumption and encourage

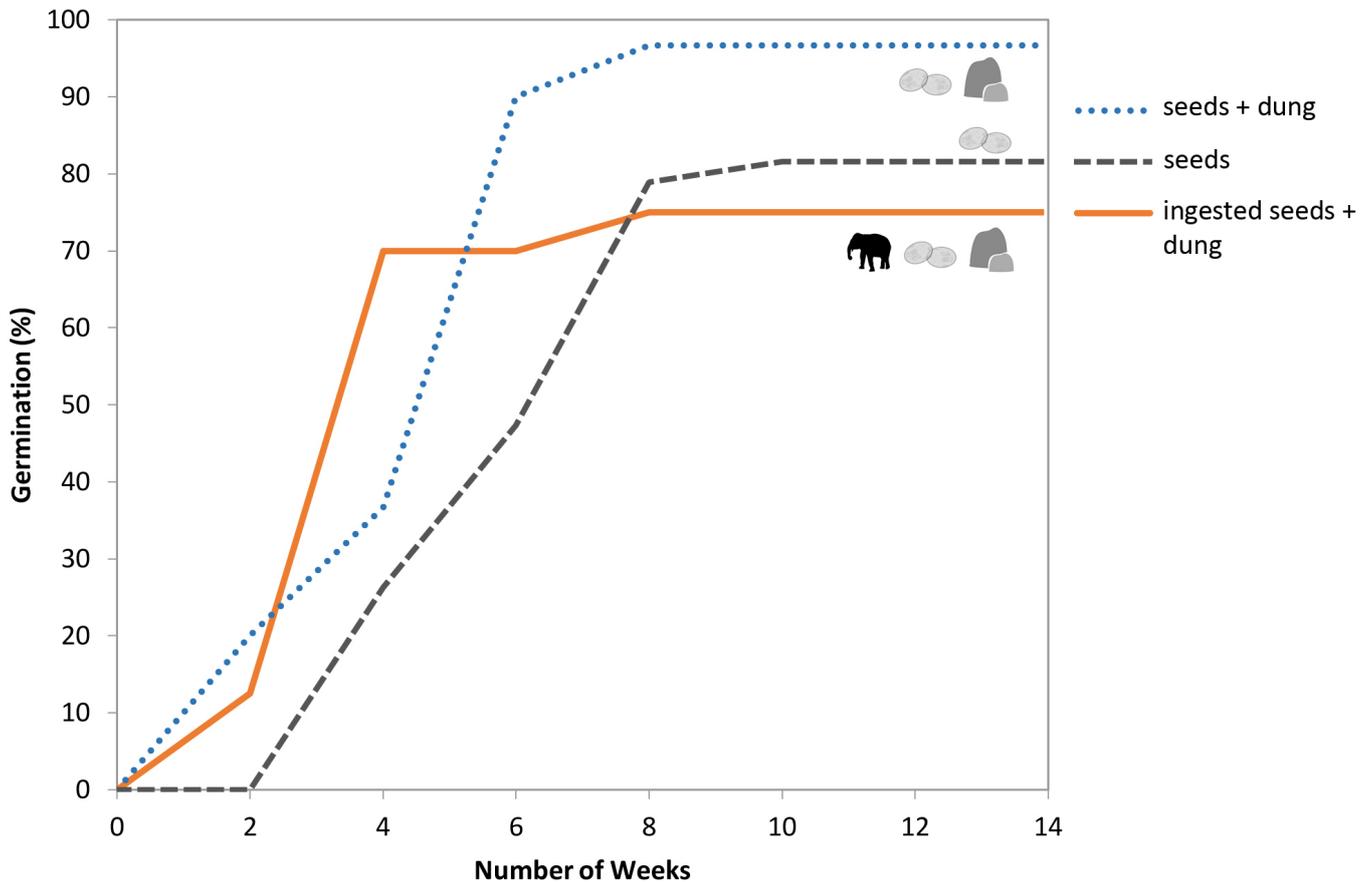


Fig. 5. Germinability of *Irvingia malayana* seeds over 14 weeks. Treatments: D+IS = elephant-ingested seeds planted in dung; D+S = depulped control seeds planted in dung; S = depulped control seeds planted in forest soil.

short visits to fruits to ensure dispersal being distributed over time. The plant might be favouring long-distance dispersal by megafauna prior to dispersal by less effective dispersers (Narconk et al., 1998; Sekar & Sukumar, 2013). While the benefits of elephants' dispersal are obvious, wild boars' seed crushing behaviour could also facilitate germination if seeds escaped when dropped (Narconk et al., 1998).

Should *I. malayana* be considered a megafaunal-syndrome species? In our sample, the fruit sizes ( $50.9 \times 42.1$  mm) of *I. malayana* match the megafaunal fruit syndrome as defined by Guimarães et al. (2008) for the Neotropics (i.e., single-seeded fleshy fruit  $\geq 4$  cm in diameter). Additionally, the fruit and seed characteristics of *I. malayana* match other traits described by Janzen & Martin (1982) for megafaunal fruits: seeds protected by a hard endocarp that survive gut digestion, pulp rich in fats, and fruits that are dull green, indehiscent, which scatter over the ground slightly before ripening. In contrast, *I. malayana* fruits in other locations are smaller. In Thailand, for example, fruits were 36.6 mm in length and 32.8 mm in diameter (Kitamura et al., 2002). It could be argued that *I. malayana* is at the fringe of the spectrum of a megafaunal-syndrome plant. It would be interesting to investigate geographical differences in *I. malayana*'s fruit and seed size and its relation with the local assemblage of dispersers.

Due to the small sample size, this study needs to be considered as preliminary. We deployed camera traps on only five *I. malayana* trees and for a short period. This is an inevitable limitation due to the difficulty to find more fruiting *I. malayana* individuals in the forest within the short fruiting period. Further studies with a larger sample size may reveal that other mammals (e.g., deer, wild cattle, tapirs, or sun bears) also contribute to the dispersal of the species. All the seeds used to test viability after being ingested by elephants were obtained from one single dung pile and therefore suffer from autocorrelation. The comparisons between germination treatments should be interpreted cautiously, but it is clear that *I. malayana* seeds dispersed by elephants retain high viability (75%, Fig. 5).

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

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