

Lost mutualisms: Seed dispersal by Sumatran rhinos, the world's most threatened megafauna

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Abstract

Diverse assemblages of seed-dispersing megafauna once existed in Asian rainforests, but are now almost solely represented by elephants. Asia's rhinos persist in remnant, ecologically extinct populations and the most threatened of these is the Sumatran rhino, *Dicerorhinus sumatrensis*. To understand the seed dispersal role of Sumatran rhinos, we consolidated information on fruit consumption, seed dispersal, and fruit traits from a 2-month field study (Sumatra), local ecological knowledge (Peninsular Malaysia), and published and unpublished accounts. We evaluated differences between the taxa and traits of fruits dispersed by rhinos and elephants, and identified other dispersers of megafaunal-syndrome fruits that were rhino-dispersed. At least 79 plant species were dispersed by rhinos: overstorey plants (trees and climbers; 78% of species) had large, usually "mammal-colored," fruits and seeds, and were mainly drupes and berries; 61% of these were megafaunal-syndrome fruits (>4 cm wide). Understorey plants (herbs, shrubs, and small trees) had small, often capsular, fruits and seeds that are potentially dispersed following the "foliage-is-the-fruit" hypothesis. Rhinos were the only known disperser for 35% of the megafaunal-fruit genera. The highest dispersal overlap shown was with elephants: fruits dispersed by rhinos tended to be capsular and were smaller than fruits dispersed by both elephants and rhinos. Given these findings and the different foraging and ranging behavior of Sumatran rhinos and elephants, we suggest that these megafauna had important differences in their seed dispersal roles. Asian rainforests have, therefore, lost an important seed dispersal mutualist. Conservation efforts should aim to protect and restore the ecological function of these unique creatures.

Abstract in Indonesian is available with online material.

KEY WORDS

ecologically extinct, megafaunal fruit, shifting baselines, southeast asia, sumatran rhinoceros, tropical rainforest

1 | INTRODUCTION

Often during the fruit season their faeces are full of the stones of jungle fruits, unbroken but clean of all fibre. Thus does the rhinoceros spread trees, useful to himself and other animals throughout the jungle. (Hubback, 1939)

The pivotal seed dispersal roles performed by the few megafauna extant today, must pale in comparison to that effected by the rich assemblages of megafauna that existed prior to global declines from the late Pleistocene (Pires et al., 2018). Much of our knowledge on the role megafauna play in seed dispersal comes from elephants in Africa and Asia (Campos-Arceiz & Blake, 2011; Hyvarinen et al., 2021). However, elephants are unlikely to represent the diversity of roles played by these past megafaunal assemblages that included animals, such as forest rhinos, giant tapirs, laminoid camelids, cave bears and extinct proboscideans with potentially varied diets, foraging, and ranging behavior (Pires et al., 2018; Saarinen, 2019).

Eurasia is the center of Rhinocerotidae diversification, and the family was one of the richest megafauna taxa in Asia, represented by more than 59 species, in 27 genera (Cerdeño, 1998; Geraads et al., 2020). Rhinos were probably once found across much of the available habitats (e.g., grasslands, swamps, and rainforests) in tropical and temperate regions, and this combined with their general herbivorous diet, suggests they were involved in essential mutualisms with plants, such as seed dispersal. Evidence for seed dispersal can be found from studies of the greater one-horned rhinos (*Rhinoceros unicornis*) in open habitats (Dinerstein, 1991) and scattered anecdotal evidence for the rainforest-dwelling Sumatran rhino (*Dicerorhinus sumatrensis*; e.g., van Strien, 1985). With a contemporary reduction in diversity to just three rare Asian species—the critically endangered Sumatran rhino and the Javan rhino (*Rhinoceros sondaicus*), and the Vulnerable greater one-horned rhino—these mutualisms have likely been lost. The National Parks of Chitwan (Nepal) and Kaziranga (India) are the only two places where the greater one-horned rhino still occurs at ecologically relevant densities (Subedi et al., 2017; Talukdar, 2013), while a dense, but very small population of Javan rhino is conserved in Ujung Kulon, Java (Indonesia) (Setiawan et al., 2017).

Sumatran rhinos have undergone a dramatic range reduction in the past 100 years (Figure 1). They once roamed from the foothills of the Eastern Himalayas, through Myanmar, Thailand, China, and Vietnam, to the Malay Peninsula, Sumatra, and Borneo (Mahmood et al., 2021; Wilson & Mittermeier, 2011). The latter two islands are the only places Sumatran rhinos are still known to occur, and they do so in tiny and fragmented populations with a global wild population estimated to be of less than 80 individuals (e.g., Gokkon, 2020). The smallest of the rhinos, at an average body weight of 775 kg, Sumatran rhinos are browsers and their diet consists of saplings, bark, twigs, leaves, and fruits (van Strien, 1985). They are considered to be very agile and adaptable to a variety of habitats, but hunting has forced much of the remnant populations into forested mountainous areas

(Strickland, 1967). Given their presence in rainforests, which provide rich fruit resources, we might expect Sumatran rhinos to have once played important roles in seed dispersal—perhaps even more than the Asian elephants, which preferentially have monocot-based diets (Campos-Arceiz & Blake, 2011). Today, elephants are the only megafaunal seed disperser remaining in many regions once occupied by Sumatran rhinos, but we could expect these two species to have played complementary, rather than redundant roles in dispersal considering these differences in diet and morphology.

Here we review knowledge on seed dispersal by the Sumatran rhino, using newly collected datasets along with published and unpublished research collected mainly from the 1960s to the 1980s. We use this consolidated dataset to determine the plants, and fruit traits once serviced by the ecologically extinct Sumatran rhino. We tested the hypothesis that seed dispersal roles provided by rhinos and elephants differed according to the traits of the plant species. We also identify other animals that have been recorded dispersing seeds of megafaunal-syndrome fruits that were noted to be rhino-dispersed. The two novel datasets on seed dispersal by Sumatran rhinos were from: (a) a brief field study on seed dispersal by Sumatran rhinos in Way Kambas National Park, Sumatra, Indonesia and (b) interviews with Orang Asli indigenous people, about seed dispersal by (the now locally extinct) rhinos in the Belum-Temengor Forest Complex, Peninsular Malaysia.

2 | METHODS

2.1 | Way Kambas Field Study, Sumatra

The field study in Way Kambas National Park was conducted across two and a half months spread between July and November 2011. Way Kambas is located in southern Sumatra, Lampung Province, Indonesia, with an average daily temperature of 25–27°C and annual rainfall of 2,500–3,000 mm. Several habitats occur within the national park, including dipterocarp lowland forest, swamp forest, mangroves, and grasslands, and altitude is 0–60 m asl (Pusparini et al., 2015). Sumatra occurs in the Sundaic region of Southeast Asia, which is noted for its community mast-fruiting cycles. Along with the Sumatran rhino, the park contains other threatened species some of which might have the capacity to disperse the same species as rhinos, including Sumatran elephants (*Elephas maximus sumatranus*), Malayan tapirs (*Tapirus indicus*), agile gibbons (*Hylobates agilis*), and sun bears (*Helarctos malayanus*).

We searched for rhino dung along 18.5 km of forest trails, walking each trail three times. For all dungs found, we recorded dung age (<12 h, 2–3 d, 3–7 d, 1 wk–1 mo, >1 mo; guesstimated by the field team based on previous experience), bolus size, habitat, and whether it was a single defecation or occurred in a latrine; rhinos often deposit multiple dungs in the same place and these are termed latrines. We searched the dungs for seeds, conducting in-situ searches for large seeds (>5 mm wide). For smaller seeds we quantified the number in a sample comprising 15% of the dung pile by mass which was

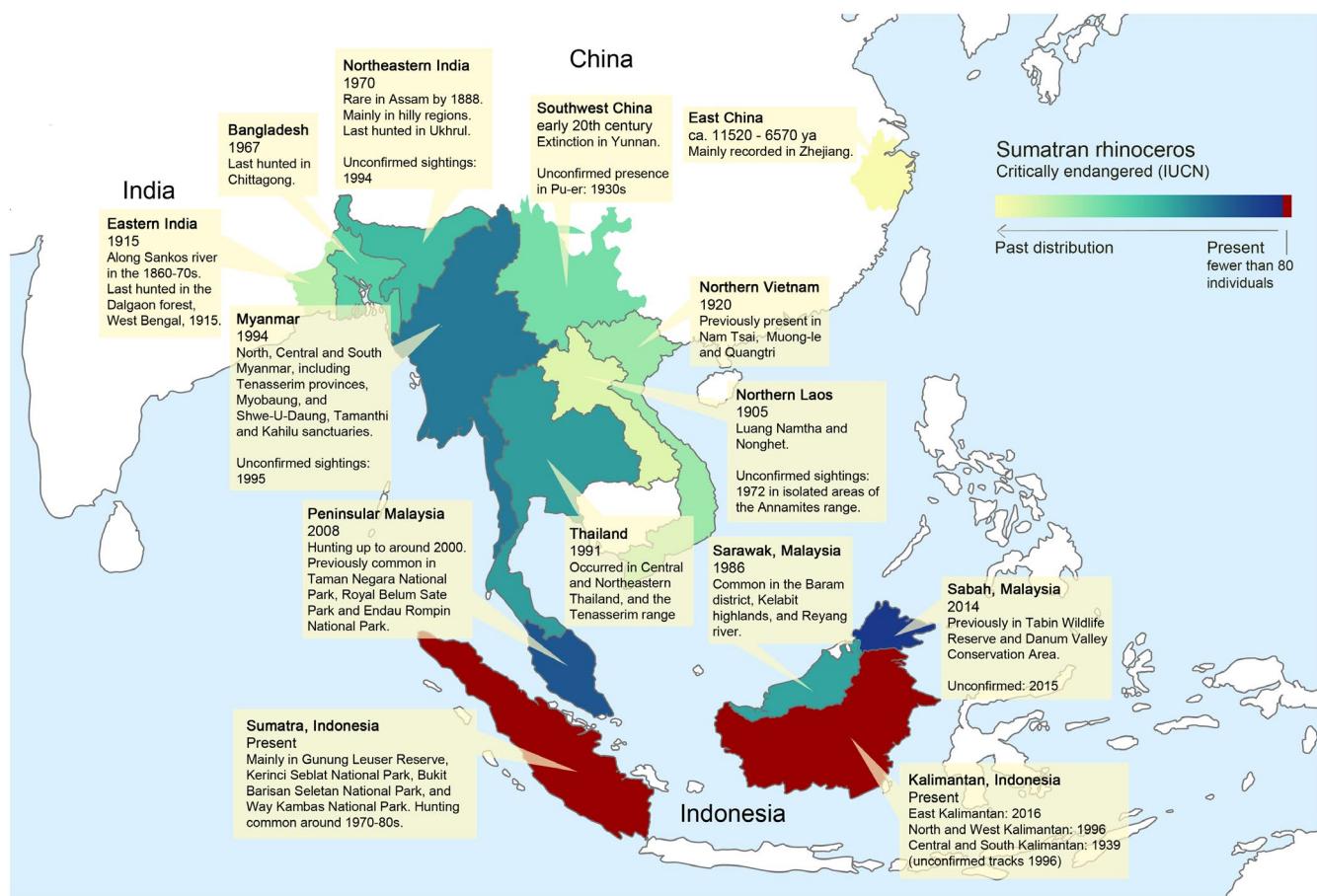


FIGURE 1 Previous and current distribution of the Sumatran rhino. For each country or region, details on the last sightings are provided in the caption. The map shows the rapid extinction of the rhinos, beginning mainly from western regions of its range in the early 20th century and accelerating in the 1960s and 70s. See Appendix S1 for references

later washed over a fine-mesh sieve. Dung mass ranged from 150 g to 3250 g, and averaged 602 ± 542 g (mean \pm SD). Seed length and width were measured. We also collected fruits from all sources we found to use as an aid to identify seeds in dung.

The irregular mast fruiting cycles (2–10 years) of Sundaic forests (Appanah, 1993) make the fruiting period difficult to predict. Unfortunately, our Way Kambas study was not conducted in a peak period in fruiting and we expect that the few seeds we found in dungs is a consequence of this. Hence, we combine our collected data with other sources to provide the most comprehensive overview of seed dispersal for this extremely rare rhinoceros.

2.2 | Interview data from Peninsular Malaysia

We documented local ecological knowledge as a second source of information to identify plant species dispersed by Sumatran rhinos. These interviews were conducted as part of a broader study on the seed dispersal network of the Belum-Temengor forest complex (Ong et al., 2021), Peninsular Malaysia, where the rhino is presumed to have gone extinct in the early 2000s (Zafir et al., 2011). Belum-Temengor is also dominated by the mast fruiting dipterocarp forests of Sundaland, with hill dipterocarp forest being most common. We

interviewed 15 Orang Asli (Peninsular Malaysia's indigenous people) from the Jahai and Temiar communities, who are very familiar with the local flora and fauna. Since only one respondent claimed to be able to identify the fruits consumed by rhinos, these results were not included in the final seed dispersal network (Ong et al., 2021) but are presented here. The respondents were asked if the animal swallowed, chewed, or discarded the seeds of each plant species identified as consumed. We also collected measurements and descriptions of the fruits and seeds in the region ($n = 164$ species), so that each rhino-fruit interaction we asked about in the interviews was accompanied by fruit and seed trait information. We recorded fruit and seed length and width, seed number per fruit, color, fruit-type, and growth form (see Ong et al., 2021 for full details).

2.3 | Publications and final data compilation for review

Finally, we reviewed previous publications on the ecology of Sumatran rhinos, mostly accounts by explorers, hunters, and scientists who visited Sumatra and the Malay Peninsula in the 1900s, and collated their accounts of the fruit diet and seeds found in dungs. We also included more recent unpublished reports written in Bahasa

Indonesia. The names of all plant species identified were checked on Kew's Plants of the World Online database and the list of species we present has the most recent names. We also collected information on the vegetative components of the rhino's diet to determine which dispersed species might also be consumed for other plant parts. We searched for information on the fruit and seed traits (see previous section for list), and plant growth form for all species identified as having the fruit consumed by Sumatran rhinos, using local floras and online sources. We determined megafaunal fruits to have a width greater than 40 mm (Guimarães et al., 2008) and categorized mammal colored fruits as colors usually associated with terrestrial mammals (green, brown, yellow, and orange) (Bunney et al., 2019; Yokoyama et al., 2005). We checked each plant species on the IUCN Red List to determine its status.

2.4 | Comparison of taxa and traits of dispersed fruits between Sumatran rhinos and elephants

We searched the literature for evidence of elephants dispersing fruits from the genera we identified as rhino-dispersed. Hence, of the complete list of rhino-dispersed plants, we distinguished those that were also dispersed by elephants (elephant and rhino-dispersed) from those that were not (rhino-dispersed). We did not identify plants that were elephant-dispersed with no record of rhino consumption due to the disproportionate amount of information available for elephants, which would bias this assessment. We compare the taxa dispersed between elephants and rhinos at the levels of genus, family and order. To compare trait selection between the animals we assumed that if elephants were recorded to consume a species within a particular genus (e.g., *Mangifera*) they would consume other species within that genus, and used species-specific trait information.

We used simple summary statistics to compare fruit traits in understorey (herbs, shrubs, and small trees) and overstorey (trees and climbers) plants fed on by rhinos (t-test, chi-square test), as well as between species dispersed by rhinos with those dispersed by elephants and rhinos.

2.5 | Identifying other dispersers of megafaunal fruits dispersed by rhinos

To assess whether any species might rely on Sumatran rhinos for seed dispersal, we searched the literature and used the community-wide, unpublished dataset of L. Ong to identify other dispersers of rhino-dispersed fruits. We focused on megafaunal fruits only because the large size of these fruits potentially makes them more reliant on rhinos for dispersal. An exception to this are smaller, very hard fruits (Dinerstein & Wemmer, 1988) but this trait information was generally unavailable. Dispersal information at the plant species level is limited for Southeast Asia, and we assume that most non-megafaunal fruits have alternative dispersers even though they

might not be identified in all instances. Our searches focused on endozoochoric dispersers (including regurgitation by deer and bovids) and stomatochory (including seeds spat by macaques, or carried and dropped by bats). We did not include synzoochoric dispersal by rodents due to the sparse availability of information. However, we recognize that this mode of dispersal might be important for very large seeds in some habitats (Jansen et al., 2012, Ong et al. in press).

3 | RESULTS

3.1 | Way Kambas Field Study

Over the 2.5 months, we found 48 dung piles from Sumatran rhinos, with dung estimated age varying from less than 2 days to more than a month. Dung piles were found in multiple habitats, with only 29% of the dungs found in latrines and 71% as single deposits. Six of the 48 dungs contained seeds (12.5% of all dungs), representing at least seven species (*Cordia dichotoma*, *Phyllanthus emblica*, *Garcinia mangostana*, and four unidentified species) (Table 1). The dungs with seeds contained around 12 seeds per dung (range of 7–21, but this is extrapolated from 15% of sieved dung weight). The largest seed found in dung was that of *G. mangostana* measured at 19.9 × 12.0 × 9.7 mm (length × width × height). The smallest was an unidentified species at 1.6 × 1.5 × 1.4 mm.

3.2 | Interview data from Peninsular Malaysia

The Orang Asli of Belum-Temengor described 32 species (25 genera) as being consumed by Sumatran rhinos (Table 1) and most of these species (29 species from 23 genera) were noted to have their seeds swallowed (rather than destroyed or discarded) (Table 1). Twenty-six of these species could be identified to species or genus level, and two species could not be identified beyond their local names (*jerantok* and *selamak*). For three species (*Parashorea* spp., *Vatica* sp., family Dipterocarpaceae) the seeds were consumed (and destroyed).

3.3 | Traits of plant species dispersed by rhinos

Altogether we compiled evidence of confirmed or probable seed dispersal for at least 79–85 plant species (some species were not identified) from at least 56 genera, 34 families, and 17 orders (Table S1). The plant families with the most dispersed species were Anacardiaceae (10 species), Moraceae (8 species), Annonaceae and Clusiaceae (6 species each). The size of fruits dispersed ranged from the small *Symplocos racemosa* (5-mm wide) to the large *Artocarpus lanceifolius* (116-mm wide); seed sizes ranged from the tiny seeds of *Ficus* to the 71-mm wide *Mangifera indica*. Fruit width averaged 43.7 ± 28.8 mm (mean \pm 1 SD), and seed width 15.1 ± 13.8 mm.

The majority of species dispersed were medium or large trees (72%), with fruits from other growth forms consumed less frequently:

TABLE 1 List of plant genera for which the Sumatran rhino is a proven (seeds noted in dung) or likely seed disperser. Synonyms of accepted species names have been updated to follow Kew's online database. Evidence includes confirmed observations of seeds or seedlings in dung (Du), mention of consumption without noting the source of evidence (Co), or interviews with Orang Asli in Peninsular Malaysia (In). Taxa for which elephants have not been recorded to act as seed dispersers are indicated by ^R

Order	Family	Genus	# spp	Identified species	Growth form	Evidence	Location	Ref.
Malpighiales	Achariaceae	<i>Hydnocarpus</i>	1		Tree	In	P. Malaysia	1
Sapindales	Anacardiaceae	<i>Bauea</i>	1	<i>macrophylla</i>	Tree	In	P. Malaysia	1
	Anacardiaceae	<i>Dracontomelon</i>	1	<i>dao</i>	Tree	In	P. Malaysia	1
	Anacardiaceae	<i>Mangifera</i>	6	<i>foetida, griffithii, indica, lagenifera</i>	Tree	Du	Myanmar, Sumatra, P. Malaysia	3, 6, 7, 8, 12
	Anacardiaceae	<i>Spondias</i>	2	<i>dulcis, priniana</i>	Tree	In, Du	Sumatra, P. Malaysia	1
Cucurbitales ^R	Anisophylaceae ^R	<i>Anisophyllea^R</i>	1	<i>griffithii</i>	Tree	Du	P. Malaysia	12
Magnoliales	Annonaceae	<i>Alphonsea</i>	1			In	P. Malaysia	1
	Annonaceae	<i>Cyathocalyx</i>	1		Tree	In	P. Malaysia	1
	Annonaceae	<i>Mezettia</i>	2	<i>parviflora</i>	Tree	Co, In	P. Malaysia	1, 2
	Annonaceae	<i>Monocarpia</i>	1	<i>mingayi</i>	Tree	In	P. Malaysia	1
	Annonaceae	<i>Platymitra</i>	1		Tree	In	P. Malaysia	1
Gentianales	Apocynaceae	<i>Alstonia^R</i>	1	<i>scholaris</i>	Tree	Du	Sumatra	10
	Apocynaceae	<i>Willughbeia</i>	1	<i>flavescens</i>	Climber	In	P. Malaysia	1
Boraginales	Boraginaceae	<i>Cordia</i>	1	<i>dichotoma</i>	Small tree	Du	Sumatra	4
Sapindales	Burseraceae	<i>Santiria</i>	1	<i>tomentosa</i>	Tree	-	Borneo	11
Malpighiales	Calophyllaceae	<i>Calophyllum</i>	1	<i>macrocarpum</i>	Tree	In	P. Malaysia	1
Malpighiales	Chrysobalanaceae	<i>Parinari</i>	1		Tree	Du	P. Malaysia	12
Mapighiales	Clusiaceae	<i>Garcinia</i>	4	<i>forbesii, mangostana, parvifolia, xanthochymus</i>	Tree	Du, Co, In	P. Malaysia, Sumatra	1, 2, 4, 6
Cornales	Cornaceae	<i>Alangium</i>	1		Tree	In	P. Malaysia	1
Dilleniiales	Dilleniaceae	<i>Dillenia</i>	4	<i>aurea, excelsa, indica, reticulata</i>	Tree	Du, In	Myanmar, Sumatra, P. Malaysia	1, 3, 10
Ericales	Ebenaceae	<i>Diospyros</i>	6	<i>confertiflora</i>	Tree	In	P. Malaysia	1
Oxalidales	Elaeocarpaceae	<i>Muntingia^R</i>	1	<i>calabura</i>	Shrub	Co	Sumatra	10
	Elaeocarpaceae	<i>Sloanea</i>	1	<i>javonica</i>	Tree	In	P. Malaysia	1
Mapighiales	Euphorbiaceae	<i>Glochidion^R</i>	1	<i>forbesii</i>	Tree	Du	Sumatra	10
	Euphorbiaceae	<i>Macaranga</i>	1	<i>tanarius</i>	Shrub	Du	Sumatra	10
Fabales	Fabaceae	<i>Parkia</i>	2	<i>sumatrana</i>	Tree	Du	Myanmar	3
Lamiales	Lamiaceae ^R	<i>Withex^R</i>	1	<i>pininata</i>	Tree	Du	Sumatra	10
Laurales ^R	Lauraceae ^R	<i>Eusideroxylon^R</i>	1	<i>zwykleri</i>	Tree	Co	Borneo	5
Ericales	Lecythidaceae	<i>Barringtonia^R</i>	1	<i>macrostachya</i>	Climber	Du	Sumatra	10
	Lecythidaceae	<i>Careya</i>	1	<i>arborea</i>	Tree	Du	Myanmar	3

(Continues)

TABLE 1 (Continued)

Order	Family	Genus	# spp	Identified species	Growth form	Evidence	Location	Ref.
	Lecythidaceae	<i>Planchonid</i> ^R	1	<i>valida</i>	Tree	Du	Sumatra	10
Gentianales	Loganiaceae	<i>Strychnos</i>	1		Climber	In	P. Malaysia	1
Malvales ^R	Malvaceae ^R	<i>Hibiscus</i> ^R	1	<i>macrophyllus</i>	Small tree	Du	Sumatra	10
		<i>Pterospermum</i> ^R	1	<i>javanicum</i>	Tree	Du	Sumatra	10
Sapindales	Meliaceae	<i>Lansium</i>	1		Tree	In	P. Malaysia	1
	Meliaceae	<i>Melia</i> ^R	1	<i>azedarach</i>	Small tree	Du	Sumatra	10
	Meliaceae	<i>Sandoricum</i>	1	<i>kotijepe</i>	Tree	Du	Myanmar	3
Fabales	Mimosaceae ^R	<i>Leucaena</i> ^R	1	<i>leucophaea</i>		Co		9
Rosales	Moraceae	<i>Artocarpus</i>	3	<i>elasticus, lancefolius, rigidus</i>	Tree	In, Co, Du	P. Malaysia, Sumatra, Borneo	1, 2, 10, 11
	Moraceae	<i>Ficus</i>	4	<i>auriculata, hispida, racemosa, uncinata</i>	Shrub, small tree, tree	Du	Myanmar, Sumatra, Borneo	3, 10, 11
Magnoliales	Myristicaceae	<i>Myristica</i>	1	<i>iners</i>	Tree	Du	Sumatra	10
Malpighiales	Phyllanthaceae	<i>Cleistanthus</i> ^R	1	<i>monoicus</i>	Shrub	Du	Sumatra	10
	Phyllanthaceae	<i>Phyllanthus</i>	1	<i>emblica</i>	Tree	Du	Myanmar	3, 4
Piperaceae ^R	Piperaceae ^R	<i>Piper</i> ^R	1	<i>aduncum</i>	Shrub	-	Borneo	11
Lamiales ^R	Plantaginaceae ^R	<i>Plantago</i> ^R	1	<i>major</i>	Herb	Du	Sumatra	10
Caryophylla. ^R	Plumbaginaceae ^R	<i>Plumbago</i> ^R	1	<i>indica</i>	Shrub	Du	Sumatra	10
Ericales	Primulaceae	<i>Embelia</i> ^R	1	<i>javanica</i>	Climber	-	Borneo	11
Rosales	Rosaceae ^R	<i>Prunus</i> ^R	1		In	P. Malaysia	1	
Sapindales	Rutaceae	<i>Citrus</i>	1		Tree	Du	P. Malaysia	12
Malpighiales	Salicaceae	<i>Flacourzia</i>	1	<i>rukam</i>	Small tree	Du	Sumatra	10
Ericales	Sapotaceae	<i>Chrysophyllum</i>	1		Tree	Co	P. Malaysia	2
	Sapotaceae	<i>Payena</i> ^R	1	<i>costata</i> ^a	Du	Sumatra	8	
	Sapotaceae	<i>Planchonella</i> ^R	1	<i>mangayi</i>	Tree	Co	P. Malaysia	2
Ericales	Symplocaceae	<i>Symplocos</i>	1	<i>racemosa</i>	Shrub	Du	Sumatra	10
Vitales	Vitaceae	<i>Leea</i>	1	<i>indica</i>	Shrub	Du	Sumatra	10
		Jerantok			In	P. Malaysia	1	
	Unidentified	Selamak ^R	1		In	P. Malaysia	1	
	Unidentified	3			Du	Sumatra	4	

Note: References for rhino: ¹Ong unpublished data; ²Metcalf (1961); ³Evans (1905); ⁴this study; ⁵Qie et al. (2019); ⁶Borner (1979); ⁷Strickland (1967); ⁸Hubback (1939); ⁹Awaliah et al. (2019); ¹⁰Rahmadi et al. (2010); ¹¹Atmokor unpubl. data; ¹²Flynn (1983).

References for elephant seed dispersal: Ong unpublished data, Kitamura et al. (2007), Campos-Arceiz et al. (2008), Joshi & Singh (2008), Jothish (2013), Tan et al. (2021).

^aThis species is not recognized on Plants of the World on-line, and the up-dated species name cannot be determined. The pulp is described by Hubback (1939) as having “thick sticky creamy juice.”

shrubs (13%), small trees (9%), climbers (6%), and herbs (1%). This diversity of growth forms suggests two categories of seed dispersal by rhino—(i) the fruit is the targeted food item, since the leaves are in the canopy or sub-canopy and not accessible to the rhinos (i.e., from trees and climbers); (ii) the fruit might be eaten along with the vegetative matter either intentionally or unintentionally. This is called the “foliage-is-the-fruit” hypothesis (Janzen, 1984) and could be achieved by rhino for plants that are herbs, shrubs, and possibly small trees (since rhinos push these down to consume the leaves).

The fruit traits of the trees and climbers (overstorey) differed significantly from the fruits in the understorey (Figure 2). The overstorey species had larger fruits (means of 48.6 vs. 20.6 mm; $t = -3.266$, $df = 67$, $p = .0009$) and seeds (16.5 vs. 3.3 mm; $t = 2.302$, $df = 54$, $p = .013$). They were also more likely to have colors believed to be more attractive to mammals (yellow, orange, green, or brown) (Figure 3) ($\chi^2 = 7.539$, $df = 1$, $p = .006$). Understorey fruits dispersed by rhinos were more likely to be capsular, while overstorey fruits had more drupes and berries ($\chi^2 = 11.533$, $df = 1$, $p = .0006$). Overstorey plants had many megafaunal fruits (61%; fruits with width ≥ 40 mm); none of the shrubs or herbs had megafaunal fruit, but two of the six small trees did. Of the 16 dispersed species in the understorey, we found confirmed observations of rhinos also eating the vegetative part of half of them. In comparison, of the overstorey plants 22 species were also consumed as young saplings (31%; Appendix S2).

3.4 | Comparison between Sumatran rhinos and Asian elephants

Around one-third of the plant taxa identified to be dispersed by rhinos were not dispersed by elephants (33% of genera, 29% of families, and 35% of orders) (Table 1). The number of taxa found in the forest understorey versus the overstorey did not differ between those dispersed by rhinos or elephants and rhinos ($\chi^2 = 1.695$, $df = 1$, $p = .192$); nor did the color of the fruit ($\chi^2 = 0.489$, $df = 1$, $p = .484$). In a comparison of fruit-types (drupe, berry, and capsular), capsular fruits tended to be dispersed by rhinos ($\chi^2 = 10.283$, $df = 2$, $p = .006$) (Figure 3).

Fruit width tended to be larger for shared fruits (elephants & rhinos, mean \pm SD; 50.32 ± 29.17) than for fruits that were rhino-dispersed (23.51 ± 15.79) ($t = -3.607$, $df = 67$, $p = .0006$) (Figure 2). Megafaunal fruits (fruit width > 40 mm) were more likely to be dispersed by both animals; 33 species of megafaunal fruits were dispersed by both animals, while four species were dispersed by rhinos but not elephants. Rhino-dispersed fruits were often large-seeded (15.81 ± 14.76 mm wide) but the size did not differ significantly from seeds dispersed by elephants and rhinos (15.99 ± 14.00 mm) ($t = -0.038$, $df = 50$, $p = .970$) (Figure 2).

3.5 | Seed dispersal of megafaunal fruits

Of 37 species with megafaunal fruits (> 4 cm wide) that we recorded to be dispersed by Sumatran rhinos, four species have no reported

endozoochoric dispersers other than rhinos (Figure 4, Appendix S3). Three of the four species that were dispersed only by rhinos were the only taxa listed as threatened or nearly threatened on the IUCN Red List (*Anisophyllea griffithii*, *Eusideroxylon zwageri*, *Planchonella maingayi*; Appendix S3); the remaining species was not listed (*Barringtonia macrostachya*). *Planchonella maingayi*, might be dispersed occasionally through seed-spitting by macaques. As dispersers, elephants overlapped with rhinos more than any other animal, sharing dispersal of 33 megafaunal fruit species and these megafauna were the only dispersers of eight species. The remaining 24 species (65%) had at least one more disperser other than rhinos and elephants, although the effectiveness of these recorded dispersers has rarely been described and might be poor for some species.

4 | DISCUSSION

We found that the critically endangered Sumatran rhinoceros is a proven or likely disperser of at least 79 plant species—a number which must represent only a fraction of the species they were once involved in mutualistic associations throughout their formerly wide geographical range. Rhinos dispersed seeds from a broad range of fruit and seed sizes, and this diversity probably reflects two disparate foraging and dispersal strategies. The large fruits that fall from canopy and subcanopy plants to the forest floor are probably deliberately consumed by the rhinos. A majority of these fruits were more than 40 mm wide, displaying colors often associated with attraction of terrestrial mammal dispersers, and are therefore classified as megafaunal fruits (Guimarães et al., 2008, McConkey et al. In press). In comparison, the fruits from understorey plants (herbs, shrubs, and small trees) were usually substantially smaller, displayed a greater variety of colors, and might have been consumed intentionally or unintentionally along with the foliage of the plant (foliage is the fruit hypothesis, Janzen, 1984). Differences in fruit traits between under and overstorey plants probably reflect the general characteristics of these growth forms; however, the inclusion of these very different fruits in the diets of rhinos suggests they might once have fulfilled very broad seed dispersal roles for these plant communities.

Since the demise of Asia's stegodonts in the late Pleistocene, the main megafaunal seed dispersers in the region have been elephants and rhinoceros (McConkey et al. In press). Some of the very large bovids can also be classified as megafauna, but they are generally considered to be infrequent seed dispersers (Sridhara et al., 2016). Today only elephants persist in scattered populations throughout most of the former range of the Sumatran rhino. Our results indicate that there was probably considerable overlap in the fruit diets of these megafauna, since 77% of species were dispersed by both animals; in particular, they shared the dispersal of most megafaunal fruits. However, fruits dispersed by rhinos (but not elephants) tended to be smaller and capsular (the latter including some fleshy capsular fruit); there are probably many other traits that we could not measure that are likely more important in defining these differences, given that selection was demonstrated at the level of plant

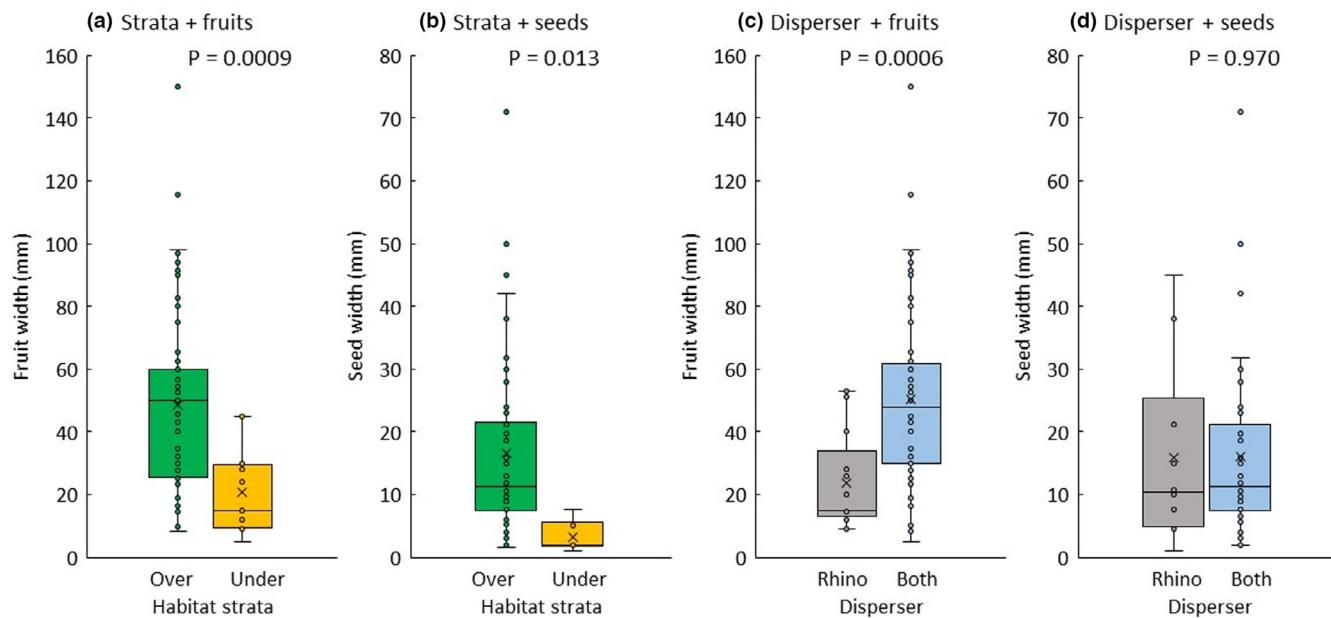


FIGURE 2 Sizes of the fruit and seeds dispersed by the Sumatran rhino. Fruits of overstorey plants (trees and climbers) are only available to the rhinos when they fall to the ground, while the fruits of understorey plants (herbs, shrubs and small trees) could be consumed directly, possibly along with foliage. Fruit width (a) and seed width (b) are larger in over- than understorey plants eaten by rhinos; around half of the fruit from overstorey sources are megafaunal fruit. Fruit width (c) was also larger in shared fruits (both rhinos and elephants) than those dispersed only by rhinos, while seed width (d) did not differ between these disperser groups

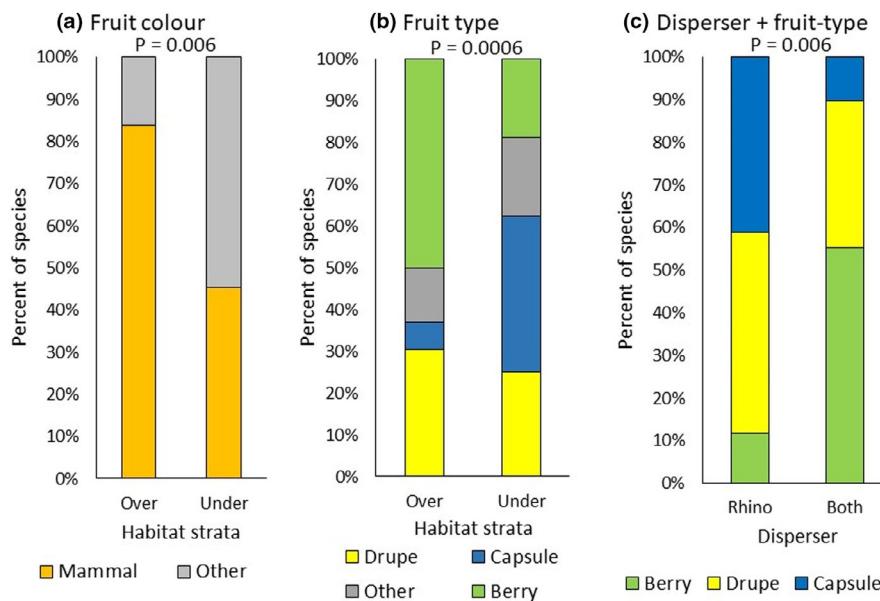


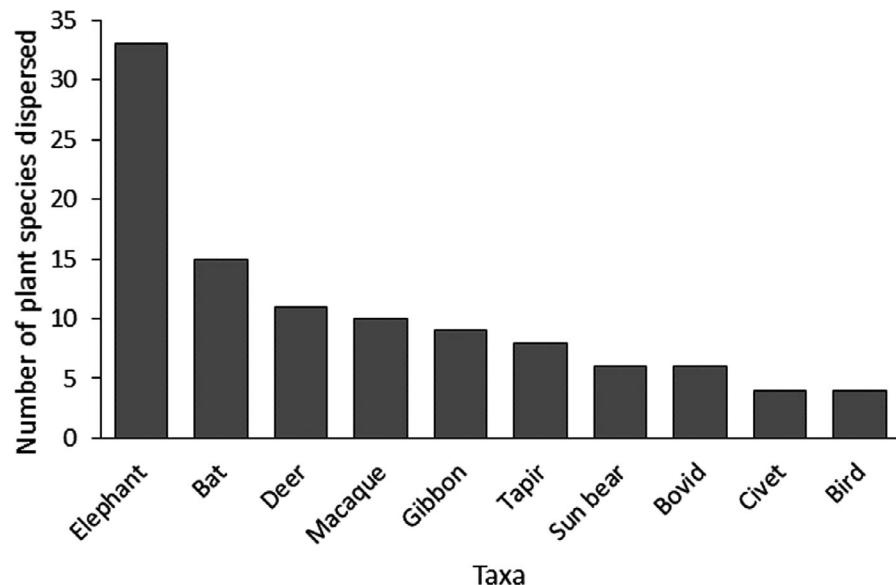
FIGURE 3 Characteristics of the fruits dispersed by the Sumatran rhino. Fruits are more likely to be mammal-colored (green, brown, yellow, and orange) in overstorey plants (a), and more capsular fruit are found in understorey plants (b). Capsular fruits also tended to be dispersed only by rhinos (c) rather than by both elephants and rhinos

orders. This suggests there are probably key differences in the dispersal roles of rhinos and elephants.

Several other attributes of Sumatran rhinos also support a conclusion that their seed dispersal behavior showed important differences to that of elephants. Elephants have massive home ranges (over 200 km² in the forests of Peninsular Malaysia; A Campos-Arceiz *unpublished data*) and tend to use major trails as they move through them. Studies on elephant-dispersed plants show low visitation rates to the fruiting plants (McConkey et al., 2018; Ong et al., 2019), and many individual plants might not be visited at all by elephants—although elephants might function as important

long-distance seed dispersers (Campos-Arceiz et al., 2008). In comparison, the home ranges of Sumatran rhinos are at least 10x smaller (estimated at 10–25 km²; van Strien, 1985) and the animals might use the landscape in a more complex way, frequently moving off the main trails and travelling up to 12 km in a day (Foenander, 1952; van Strien, 1985). We could expect Sumatran rhinos to visit more individual plants of selected species and have a higher re-visit rate, thereby increasing their reliability as dispersers. Indeed, frequently visited fruiting trees can have clearly defined rhino trails leading to them (Flynn, 1983). Rhinos also show great agility and can access rugged, mountainous areas, clambering up near vertical inclines

FIGURE 4 Overlap in seed dispersal of megafaunal fruits (>4 cm width) between the Sumatran rhino and other major dispersers. Thirty-seven plant species with megafaunal fruits dispersed by the Sumatran rhino could be compared; of these four had no other recorded dispersers. Several taxa listed include multiple species within a single habitat (e.g., deer include sambar, muntjac, and mousedeer). Bovid includes wild and domestic animals



(Borner, 1979; Evans, 1905; Hubback, 1939), reaching areas inaccessible to elephants.

The loss of Sumatran rhinos likely has different impacts on understorey and overstorey plants, with potentially the highest impact on megafaunal-syndrome plant species. Megafaunal-syndrome plants were mainly found in the overstorey, and four of the species had no recorded endozoochoric dispersers other than rhinos. Three of these species had a threatened or near-threatened IUCN Red List status (and the fourth was not listed on the Red List), which could reflect the ecologically extinct status of the Sumatran rhino. Maintaining populations of these plant species may require the recovery (by means of reintroduction) of rhino populations, or assisted dispersal by humans (Maschinski & Albrecht, 2017; Raviknanth et al., 2018). A further eight species were only dispersed by elephants and rhinos, and they might complement each other in their dispersal roles in terms of the seed shadows generated. In comparison, rhino declines have had less impact on the recruitment of smaller-fruited, understorey, plants. A prediction of the “foliage-is-the-fruit” hypothesis is that plants with fruits which are consumed inadvertently by herbivores, should be consumed by many species (Baltzinger et al., 2019; Janzen, 1984). The diet of forest-dwelling herbivores in Southeast Asia is poorly known, but it is possible that the recruitment of these species is maintained where herbivore populations have not been severely decimated.

For both understorey and overstorey plants, the impact of rhinos on plant recruitment would have also varied along the mutualism-antagonism spectrum in different ways. For understorey plants, rhinos must have often consumed both the vegetative matter (antagonism) and the fruits (mutualism) at the same time; this was suggested for 50% of the species they dispersed and this behavior has been observed in several other herbivores (Baltzinger et al., 2019; Blanco et al., 2019). Similarly, while rhinos only had access to the fruits of overstorey plants (mutualism), they also consumed the saplings of at least 31% of the same species (antagonism). Hence, rhinos could have been promoting plant diversity by both dispersing seeds

and contributing to negative density-dependent sapling mortality (Forristier et al., 2019).

Sumatran rhinoceros are browsers, consuming a diversity of plant parts (Earl of Cranbrook, 1987; Prater, 1965). Fruit consumption has sometimes been considered relatively rare (van Strien, 1985), while other researchers consider rhinos to be fond of fruits (Evans, 1905; Prater, 1965) often traveling long distances to reach favored species (e.g., *Garcinia*, Metcalfe, 1961), and with rhino trails leading to fruiting sources (Flynn, 1983). Indeed, they are described as liking sweet, soft fruits, which they can consume in large quantities (Cherang personal comment, from interviews in Belum-Temengor). The discrepancy in observations of fruit-feeding, likely reflects the irregular fruiting phenology of Sundaic forests (Appanah, 1993) and the irregular appearance of seeds (particularly large, conspicuous ones) in dung. This has been shown for elephants in Sundaic forests (Tan et al., 2021). Yet, even the low rate of seed-containing dungs that we recorded (12.5%) in a non-fruiting period, and the 15% of rhino dungs recorded to contain large seeds by Flynn (1983), is similar to that reported for elephants (19.5% including fruiting seasons, although without sieving the dung; Tan et al., 2021). These observations suggest that rhinos have a similar or potentially greater tendency for fruit consumption than elephants. Rhinoceros are probably effective dispersers for most consumed species because of their gentle gut (Sridhara et al., 2016) and observations of seedlings in the relatively few dung recorded (Flynn, 1983; Strickland, 1967; van Strien, 1985). As mega-herbivores, large defecations weighing up to 23 kg deposited by the larger greater one-horned rhinos could potentially contain thousands of seeds (Dinerstein & Wemmer, 1988). However, their dentition is similar to the smaller-bodied tapirs which destroy the seeds of many consumed fruits (Campos-Arceiz et al., 2012), suggesting seed predation can also occur for a fraction of seeds depending on seed traits.

There are other interesting aspects of the rhinos seed dispersal role which can no longer be confirmed given their extreme rarity. Sumatran rhinos once used a range of habitats, including

mountainous areas and swamps (Evans, 1905; Groves & Kurt, 1972; Metcalfe, 1961), probably creating complex and potentially directional (up or down mountains) or seasonal seed shadows (Naoe et al., 2016). They favored foraging in small forest gaps (Flynn, 1983), and might have played important roles in forest regeneration. The seed dispersal distances achieved were likely to be long with home range diameters of up to 3.5 km (Groves & Kurt, 1972) and less common long-distance movements of up to 40 km (Borner, 1979). Sumatran rhinos rely on wallows which they visit very frequently (van Strien, 1985). Further, recursive foraging by herbivores includes revisit of foraging sites and re-browsing of plants as a foraging strategy (English et al., 2014). These regular visits to a few locations within their home ranges might lead to a concentration of fruiting trees growing around them. Rhinos also form a mosaic of latrines and single dung depositions (Evans, 1905), creating varied microsite characteristics for seeds. Finally, the Sumatran rhinoceros is the “hairyest” rhino species and frequently wallowed in mud-baths (Metcalfe, 1961) and, therefore, might have dispersed many seeds by epizoochory as well (Baltzinger et al., 2019).

Until recently, the Sumatran rhino was widespread across tropical Asia, but is now extinct or ecologically extinct throughout this range. Today the population numbers are estimated to be less than 80 individuals on Sumatra, and scattered, unconfirmed individuals on Borneo (Gokkon, 2020). The Sumatran rhino's decline results mainly from poaching for the medicinal value that is mistakenly attributed to all parts of the animal, and in particular the horn (Metcalfe, 1961; van Strien, 1985) and more recently as a consequence of the fragmentation and small size of its population, and risks of reproductive pathologies in females as a result of extended isolation (Kretzschmar et al., 2016). The demise of this magnificent animal has likely resulted in loss of seed dispersal mutualisms and more complex seed shadows of megafaunal plants than can be achieved by elephants. While we often use elephants as a proxy to understand seed dispersal by megafauna, it is essential we do not forget the roles of other megafauna that were essential seed dispersal mutualists until very recently. Tropical Asia has lost 60% of its megafaunal seed dispersers since the Late Pleistocene (McConkey et al. In press) and is on the way to losing its forest rhinos (e.g., Campos-Arceiz & Lim, 2019). Conservation efforts should aim to protect, and wherever possible restore, populations of these unique creatures and their ecological functions.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Conceptualization: KRM, FA, LO, ACA; Investigation: all authors; Data curation: KRM, LO; Funding acquisition: KRM, FA, ACA; Visualization: LO; Writing original draft: KRM; Writing review & editing: KRM, LO, ACA.

ETHICAL APPROVAL

The interviews in Malaysia complied with ethics requirements of the Science & Engineering Research Ethics Committee, University of Nottingham Malaysia (permits #LO081016 and #LO200218). Prior and informed consent was obtained from village heads and all participants in the interviews, after full disclosure of the goals and planned use of the research data.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.xsj3tx9gv> (McConkey et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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