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Review

A Review of Human-Elephant Ecological Relations in the Malay Peninsula: Adaptations for Coexistence

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Abstract: Understanding the relationship between humans and elephants is of particular interest for reducing conflict and encouraging coexistence. This paper reviews the ecological relationship between humans and Asian elephants (*Elephas maximus*) in the rainforests of the Malay Peninsula, examining the extent of differentiation of spatio-temporal and trophic niches. We highlight the strategies that people and elephants use to partition an overlapping fundamental niche. When elephants are present, forest-dwelling people often build above-the-ground shelters; and when people are present, elephants avoid open areas during the day. People are able to access several foods that are out of reach of elephants or inedible; for example, people use water to leach poisons from tubers of wild yams, use blowpipes to kill arboreal game, and climb trees to access honey. We discuss how the transition to agriculture affected the human–elephant relationship by increasing the potential for competition. We conclude that the traditional foraging cultures of the Malay Peninsula are compatible with wildlife conservation.

Keywords: Asian elephants; human ecology; hunter-gatherers; niche partitioning

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1. Introduction

Elephants (Order: Proboscidea) evolved some 60 million years ago. Over this period, the elephant order included 10 families, 42 genera, and 175 species, including the woolly mammoths (*Mammuthus primigenius*), mastodons (*Mammut* spp.), stegodons (*Stegodon* spp.), gomphotheres (*Gomphotheriidae* spp.), and the straight-tusked elephant (*Palaeoloxodon namadicus*)—possibly the largest land mammal to have ever lived [1,2]. Prior to the expansion of early humans during the Pleistocene, these proboscids had no natural predators and dominated landscapes across four continents, from the Palearctic to South America [3,4]. However, in the Anthropocene, elephants' dominant ecological position has been displaced by humans. By hunting elephants and modifying natural systems, we have caused the loss of elephants throughout most of their natural range [5–9]. Elephants are now a global priority "flagship" taxon for conservation, due to their ecological importance, evolutionary uniqueness, charismatic nature, and endangered status [8,10]. Ensuring the local acceptance of the continued presence of elephants is thus one of the most significant conservation challenges in the world's remaining elephant landscapes [8].

The prehistoric experiences of the Americas [11] and Europe [12], and the history of civilisation in Egypt [13] and China [14], suggest that it is difficult for elephants and people to coexist. Elephants tend to be eliminated as civilisations became established [14]. In many parts of Africa, we (i.e., *Homo sapiens* and proboscidean species) have been described as being "complete competitors" [15]. The fact that interference competition can result in us killing one another suggests that in many instances we cannot share the same range [15]. In central Africa in particular, it has been said that elephants and human agriculture "each suffer from the presence of the other when they occupy the same forests" [16]. Because we often eat the same plants, the planting of attractive crops in landscapes occupied by elephants often leads to costly depredation and a cycle of reprisals that culminates in both people and elephants being killed. Ultimately, the local elephant population tends to be extirpated or removed from the landscape [8]. In the case of the Asian elephant (*Elephas* maximus), the species is now threatened with extinction [8] after having lost 95% of its historical range [17].

Despite the conflict that broadly characterises human–elephant relations, there are parts of the world where people and elephants have managed to live together for millennia. People in these places tend to be non-agriculturalist hunter-gatherers. In African Congo, the Mbuti people coexist with the African forest elephants (*Loxodonta cyclotis*; [18]). Similarly, in Asia, the Menraq people live alongside Asian elephants in the rainforests of the Malay Peninsula. An understanding of the ecological factors that have allowed such coexistence may help in managing the human-elephant interface in areas experiencing conflict.

With the aim of developing a broad and interdisciplinary understanding of human-elephant interactions, which can help creating a firm basis for measures to conserve elephants in coexistence landscapes, we carried out a review of the literature to identify the main ecological drivers that underpin traditional human–elephant relations in the forests of the Malay Peninsula. Our objectives include examining the extent to which people and elephants influence each other's ecology. We look at the realised ecological niches of both species in terms of (i) space (habitat); (ii) time (diurnal and seasonal activity patterns); and (iii) energy capture (feeding behaviour).

2. Methodology

2.1. Study Site

One place where humans and elephants have coexisted for at least 50,000 years is the Malay Peninsula [19]. The Peninsula runs around 1500 km down from Thailand to Singapore (7°–1° North, 99°–104° East) (Figure 1). It is presently the southernmost point of the Eurasian supercontinent but during the numerous glacial maxima of the last 2.6 million years sea levels dropped to around 120 m. At that time, the mainland was connected with the islands of Borneo, Sumatra, and Java to form the landmass known as Sundaland. The Malay Peninsula is generally hilly, with narrow coastal plains making way for a series of mountain ranges, the highest peak being Mount Tahan at 2187 m. The climate and vegetation of the Peninsula have seen dramatic change over the past 10,000 years. At the time of the last glacial maximum, around 20,000 years ago, the Peninsula was covered mainly by grasslands and savanna. However, the melting of the polar ice led to a rise in sea levels and the flooding of the South China Sea, which means that annual monsoonal north-easterly winds bring around 3000 mm of rainfall each year, causing evergreen rainforest to expand to almost completely cover the Peninsula [20,21].

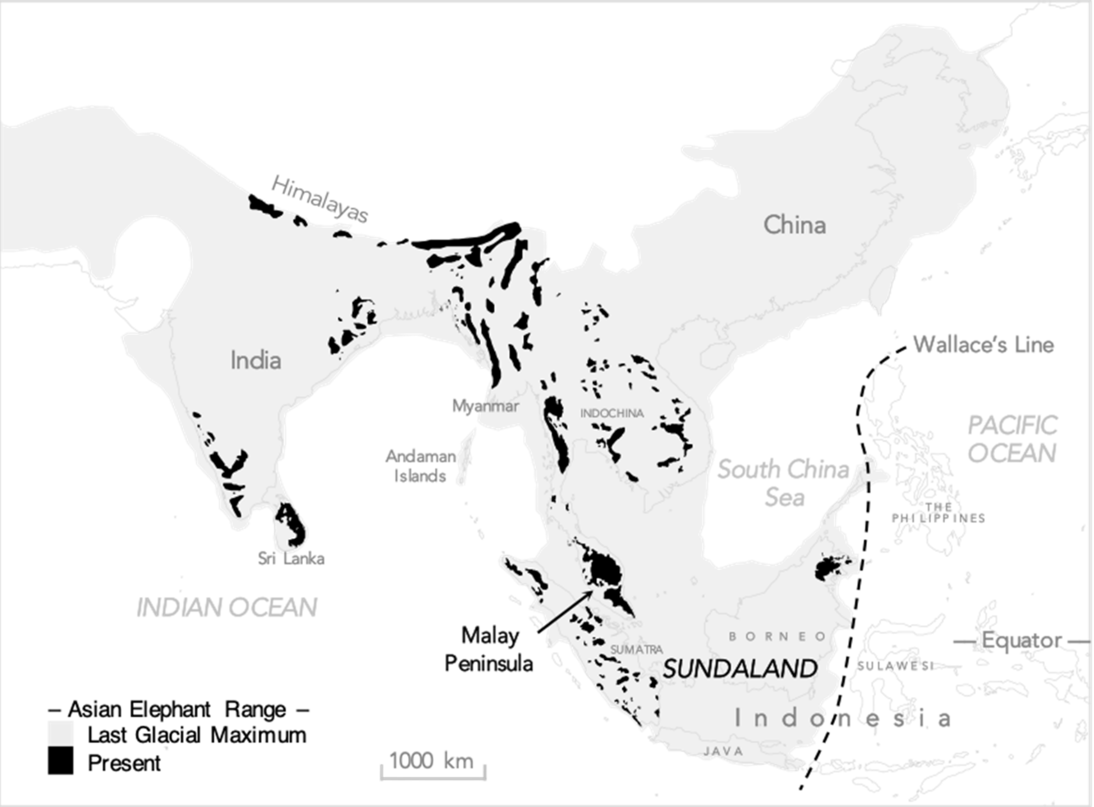

Figure 1. Approximate range of Asian elephants at the last glacial maximum (25,000–15,000 years ago), and at present. Note: The species ranged west to Turkey (not shown on this map). Reprinted from Ref: [8,22]. Made with Natural Earth.

2.2. Study Species

The elephant genus *Elephas* originated in Africa in the Miocene (around 7 million years ago) and spread to Asia during the Pliocene (around 3.7 million years ago) [23–25]. About the same time as the emergence of *Homo sapiens* in Africa around 250,000 years ago, the Asian elephant emerged in what is modern-day Myanmar. *E. maximus* is one of six proboscidean taxa known to have inhabited Pleistocene Sundaland [26]. By around 125,000 years ago, *E. maximus* had dispersed throughout Asia, reaching as far as Java in the south, and what is now Beijing in northern China [14,27–29] (Figure 1). At that time there were already several hominin species in the region, including Denisovans, *Homo erectus*, *H. floresiensis*, and *H. luzonensis* [30]. One of the reasons that the Asian elephant survived to the present is its ecological flexibility [26,31–34]. Although the Asian elephant prefers to eat grasses, it is also able to survive in the jungle by browsing on other vegetation and, in particular, by eating palms [35–37]. As a result of the arrival of anatomically modern humans in Asia, it is likely that, in response to increased hunting pressure and the use of fire, the Asian elephant survived by retreating into the forest—and only at night being brave enough to enter open clearings to graze [38]. Proboscideans that had less ecological flexibility (either behaviourally or in diet) did not survive to the Holocene [31–34].

In parallel with the early elephants, several species of early hominin, such as *Homo erectus*, are believed to have gone extinct in Southeast Asia with the loss of the savannah and the expansion of the closed-canopy rainforest during the Late Pleistocene [32,39]. In contrast, *Homo sapiens* is claimed to have had a greater degree of ecological tolerance and adaptive plasticity that allowed it to flexibly shift to life in the rainforest [40].

Settlement of the Malay Peninsula by anatomically modern humans began around 55,000 years ago, and subsequent cultural influences have resulted in a patchwork of indigenous groups, collectively referred to as "Orang Asli", occupying different parts of the Peninsula [19]. In 2010, the Orang Asli numbered around 178,000, which is less than 1%

of the current population of the Peninsula [19]. The Orang Asli include at least 20 distinct sub-groups that can be clustered into three broad cultural groups: the Menraq foragers, the Senoi swiddeners, and the Aboriginal Malay settlers [19]. Menraq groups continue to practice foraging in several parts of the lowlands of the north of the Peninsula. However, in the central highlands, swidden agriculture has been the main land use for the past 5000 years or so [41]. In contrast, the last few hundred years have seen the expansion of permanent agriculture in the coastal lowlands. Tree plantations (rubber and oil palm) now cover most of the arable land of the Peninsula [42].

2.3. Literature Review

We integrated data from a literature review with field observations. The literature review involved searching for references on human–elephant interactions using databases (including Scopus, Web of Science, Google Scholar, Google Books, and Internet Archive). The literature related to the interactions of humans and elephants in the Malay Peninsula from a wide range of disciplines, dating back to the colonial period. For context, we supplemented the results with examples from elsewhere in Asia, and also from Africa. We also included a comparison of the ecological characteristics (food, habitat, and activity patterns) of elephants and human foragers with those of tigers (the apex predator in the system). We referred to both ethnographic and ethno-historical sources. The latter included a small number of colonial-era accounts that we have cited, while recognising the tendency for such sources to be exaggerated [43], biased towards the colonial-capitalist discourse of the period [44], and to lack an explicit consideration of their positionality and reflexivity. We followed Agam and Barkai [3] in considering that, although such sources should be treated with caution, they can still be of use.

2.4. Field Observations

The field observations were made between 2015 and 2019, and included visits to 40 villages in Peninsular Malaysia. These villages included 24 villages inside the current elephant range, and included seven Menraq villages, 19 Senoi villages, and seven aboriginal Malay villages. Participant observation included joining villagers chasing an elephant out of a vegetable patch; and running away from an elephant encountered on a forest trail. We met with 58 people and carried out both semi-structured interviews with key informants and held open-ended focus-group discussions.

2.5. Analysis

We analysed the potential effect of the presence of elephants on the realised niche of early humans in the Malay Peninsula using the logic of contraposition to examine the effect of the absence of elephants (by reference to sites such as Sarawak). We examined the extent to which several aspects of local forager culture appear to be adaptive to the presence of elephants, taking a functionalist approach guided by the principles of ecological anthropology [45] and genetic determinism [46]. We present the results of the analysis of the ecological overlap and partitioning in three sections: (i) an overview; (ii) spatio-temporal niches; and (iii) trophic niches. In each section we discuss the results in the context of the wider literature.

3. Overview of the Human–Elephant Ecological Overlap

Several physiological and behavioural similarities between humans and elephants [47] mean that we have fundamental ecological niches that have a significant overlap, despite both species belonging to different mammalian orders and the existence of clear differences. Humans and elephants are both fairly generalist terrestrial megafauna with complex social behaviour and cognitive skills, and life history strategies that invest heavily in longevity rather than in producing a large number of offspring, i.e., we are “K-selected” [47]. This niche overlap can lead to ecological competition and, ultimately, intense conflicts between both species.

Given the risks associated with encountering elephants and other dangerous animals (particularly tigers, *Panthera tigris*), the Orang Asli people of the Malay Peninsula employ various means to avoid direct encounters with them. The primary means is to avoid being in the same place at the same time as elephants. Table 1 presents an outline of the spatio-temporal niche partitioning between people and other apex megafauna in the Malay Peninsula. In short, elephants and tigers are obligate terrestrialists that, in the presence of people, avoid open areas during daytime. Humans are facultative arborealists and avoid the forest floor at night, relying on trees to avoid encounters with the animals. In Section 4 we elaborate the mechanisms that elephants and humans have used in the Late Quaternary to partition our spatio-temporal niches in the Malay Peninsula.

Table 1. Spatio-temporal niche partitioning of apex megafauna (humans, elephants, and tigers) in the Malay Peninsula during the Late Quaternary. Humans are facultative arborealists, whereas elephants and tigers are obligate terrestrialists; humans avoid forest floor at night; elephants and tigers avoid open areas during the day. This table outlines Section 4 of this paper (the numbers of which are noted in bracket)).

	Activity Pattern (Section 4.4)	
Habitat (Section 4.1)	Day	Night
Arboreal (Section 4.3)		
Terrestrial (Section 4.2)		

Section 5 of this paper addresses food resource overlaps between people and elephants in the rainforests of the Malay Peninsula and the mechanisms used for niche partition (summarised in Table 2). Humans and elephants have succeeded in partitioning the use of trophic resources such as starches (palms and yams), fat and protein, and sugars (honey and fruit), enabling a degree of coexistence.

Table 2. Trophic strategies of apex megafauna in Malaysia during the Late Quaternary. Notes: *"Animals in holdes" includes porcupines, pangolins, hornbills, etc. Sources: various, including [36,48,49]. This table outlines the subsections of Section 5 of this paper (the numbers of which are noted in brackets).

Food Source (Section 5 of This Paper)	 **Elephants**	 **Humans**	 **Tigers**
Plants			
Fruit (e.g., durian: Section 5.5)	⬤	⬤	•
Leaves, stems (palms: Section 5.2, grass: Section 5.6)	⬤	•	○
Roots (tubers: Section 5.3)	•	⬤	○
Animals (Section 5.7)			
In trees (birds, squirrels, monkeys, honey (Section 5.4))	○	⬤	•
On the ground (pigs, deer, bovids)	○	•	⬤
In holes*; 'lots of little things' (grubs, snails, fish)	○	⬤	•

Key: ⬤ typical; • occasional; ○ never or very rare.

4. Spatio-Temporal Niche Overall and Partitioning: The Elephant and the Person in the Room

4.1. Eurytopic Sympatry: From Coast to Mountain Crest

Studies in India, Indonesia, and Java show that Asian elephants can occupy a wide range of habitats, although they cannot survive in extremely dry environments [50]. When modern humans (*Homo sapiens*) first arrived in the region, they probably found that elephants were already present across most of the dry land, from the coastal mangroves to the montane forest, 2000 m above sea level [36].

Although elephants and people are generalist eurytopic species (i.e., we can survive in a wide range of habitats), we do have habitat preferences that include aspects of altitude and topography. Although able to climb the highest peaks of the Malay Peninsula, we both prefer flat terrain at lower altitudes. Elephants in Malaysia's montane forests are generally lone males, as solitary elephants are better able to exploit sparse foods than are groups [38]. Similarly, human communities in the Peninsula usually camp on flatland in the valleys, and trips to less hospitable terrain are normally the preserve of males—out hunting alone or in very small groups [51,52]. Endicott and Bellwood [53] note that the Bateks (a sub-group of the Menraq) claim to be able to subsist in all types of forest except montane forest (*te' langeh*)—where they can only sustain themselves during the fruit season.

Elephants and people also prefer semi-open habitats such as along the coast, on the banks of large rivers, and as afforded by gaps in the canopy created by tree-fall, by topography, and by latitude [51,52,54,55]. These areas often have rich soils and the open canopy of early seral forest allows for food plants that support both species (see Section 5.3). For similar reasons, the wet seasonal evergreen dipterocarp forest/Schima-bamboo forest of the northwest of the Peninsula [56] has a significantly higher carrying capacity for elephants than the mixed dipterocarp forest that dominates most of Sundaland [36]. As the climate changed since the last glacial maximum, grazing by elephants might have slowed the advance of the rainforest [36,57].

4.2. Shared Pathways: Elephant Forest Trails

As they move through the forest, elephants create and maintain pathways that connect the places they frequent, such as salt licks, fruit trees, and bathing spots [58]. These routes usually follow the most accessible topography [59,60], and elephants' movement and feeding along the paths clear them of vegetation. The smaller animals of the forest, including humans, can then use these pathways (and locate and acquire the resources along them), and their actions in turn also contribute to keeping the paths open [61].

In closed-canopy tropical rainforest, calories are scarce (see Section 5), and thus ease of movement is critical. In Africa, Kingdon [62] suggests that elephant paths were crucial for the evolutionary survival of other mammals, "especially flesh-footed, soft-toed hominins". Laden [18] found that the Mbuti people of the Congo made use of African forest elephants (*Loxodonta cyclotis*) trails. Interestingly, the Mbutis were wary of following elephant trails up steep stretches as they feared meeting an elephant going down: "An elephant going down the steep slope cannot turn around and go back, so it is likely to become upset and trample any people going up the trail." Laden [18] also found that elephant trails were inappropriate for people in wetlands and at stream-crossings, as elephants tended to favour the swampiest areas, and the deepest parts of the streams.

In Asia, elephant trails have also been important for humans to access the forest. Keil [63] highlights how elephant paths enabled the human occupation of difficult upland terrain through the interconnected hilly range extending from India to South China. In the Malay Peninsula, Lye [52] notes that the Batek people preferred living in standard lowland forest (*həp ləy*) as it was the easiest kind of forest to travel in "simply because elephants also use *həp ləy* and they open up passageways that people can then use". Indeed, we found that most groups of Orang Asli appreciate the fact that elephants keep paths through the forest accessible [64].

Although elephants and other megafauna keep pathways clear, they also disperse seeds alongside these routes [61,65]. Their role as dispersers of large-seeded and large-fruited trees [66,67] means that elephants' dung alongside a pathway can enrich the vegetation that grows on the sides of the path, and thus make such routes doubly attractive for people. Non-elephant frugivores (including humans) using the trail can also contribute to this enrichment as they scatter the seeds of fruit that they themselves eat while walking along the trail—to the mutual benefit of all (see Section 5.5).

4.3. Facultative Arborealism

As with other great apes, people can escape from danger by climbing trees. Particularly at night, when great apes rest but predators are active, it is safer to nest in inaccessible locations such as up trees [68–70]. Among modern humans, above-the-ground resting places are found in many parts of the world and serve several additional functions, including safety from floods, ventilation, and protection against termites [71]. Where elephants are present, protection from them can be a major reason people build tree houses [72,73]. In the Malay Peninsula, all groups of Orang Asli occasionally construct above-the-ground shelters, usually as temporary retreats (from elephants, tigers, and from other people), and as a means of guarding crops (Table 3 and Figure 2). Tree houses built for protection against other people tend to be much higher than those used to evade elephants and tigers (as seen by examples from New Guinea and the Philippines, where wild elephants and tigers are absent).

Table 3. Above-the-ground shelters of the Orang Asli and other groups.

Group	Height Above Ground	Rationale Given	Period & Ref.
Korowai, New Guinea	35 m	slavers, "cannibals"	20th century [74]
Illongot, Luzon	18 m	head-hunters	20th century [75]
Temuan, Selangor	9–12 m	elephants	ca. 1900 [76]
Aboriginal Malays	9 m	not given	19th century [77]
Semai, Pahang	4.6–6 m	not given	19th century [78]
Semelai, Pahang	4 m	tigers, elephants	1980 (R. Gianno pers. comm., 24 July 2021)
Temuan), Selangor	3.7 m	elephants	19th century [79,80]
Temiar, Perak/Kelantan	3 m	tigers, slavers, elephants	20th century [64,81]
Jakun, Johor	1.5–2.7 m*	elephants, tigers	ca. 1900 [76,82]
Menraq (in cliffs and "large" trees)		elephants, tigers	ca. 1900 [51,76,83]
Semai (in the "sturdiest longhouse")		elephants, slavers	ca. 1960 [84]

NB. Asian elephants' average shoulder height ranges from 2.3 to 2.9 m, with the world record at 3.4 m [85]. Kelantan, Perak, Johor, Selangor, and Pahang are states in Peninsular Malaysia. *In localities where elephants abounded the houses were generally built high up.

Figure 2. Hokin Sujin (a member of the Semelai swiddener community) with his shelter (*ponong*) used for weekly keruing (*Dipterocarpus*) oleo-resin tapping at Kemiyan, Tasek Bera, Pahang, 1980. (Photograph by Rosemary Gianno, Orang Asli Archive, Mason Library, Keene State College, reproduced with permission).

4.4. Temporal Niche Partitioning: Diurnal & Nocturnal Activity Patterns

Elephants and people also tend to avoid one another by moving around at different times: people during the day and elephants at night. In the 1970s, a study by Olivier [36] in the Malay Peninsula noted that elephants tend to travel around and feed in the open at night. and feed and rest in closed forest during the day. The study suggested that this behaviour is partially in response to human predation, noting that, even during the evening, groups of elephants alerted to danger might bunch initially, but in response to a severe threat would disperse into the forest. In Belum-Temengor, a recent study by Hii [86] placed camera traps next to a salt lick where human visits peaked from 10:00 to 12:00 and found that elephants were most active from 20:00 to 06:00. Similarly, using GPS telemetry from 17 collared elephants we found that 81% of the elephant road crossing in this landscape happened at night [59] and that the activity of a crop-raiding elephant peaked between 21:00 and 23:00 when she was moving near human settlements [64]. This is consistent with findings from Asian elephants in Sri Lanka [87] and Assam [88], where crop-raiding occurred almost exclusively at night.

In contrast, several anthropological studies in the late 20th century found that the Orang Asli seldom leave their camps after dark. Robarchek and Robarchek [89] noted how the Semais could not imagine spending a night alone in the forest. Similarly, Dunn [80] noted that the Temuan sub-group of the Aboriginal Malay Orang Asli are reluctant to sleep alone in the forest for fear of evil spirits. Rambo [41] suggested that this ideology is an example of adaptive behaviour as it actually protects them from dangerous wild animals. Dunn [80] mentioned that elephants and tigers would have been the main threats to the Orang Asli in the past, with leopards and pythons as supplementary causes for concern.

5. Trophic Niche: One Bite at a Time

5.1. Finding Food in the Rainforest

In addition to avoiding bumping into each other, people and elephants in the Malay Peninsula also had to find food. In Sundaic primary rainforests, filling both human and elephant nutritional requirements (Table 4) posed difficulties because—despite an abundance of greenery—most of the biomass in the jungle is locked up in wood and in tannin-rich leaves which neither species is able to digest [90–92]. Additionally, key food sources such as fruits are largely seasonal or unpredictably available [20]. Closed-canopy primary rainforest is thus marginal habitat for both humans [93] and elephants [36,54,59].

Table 4. Daily energy and protein requirements of elephants and people.

	Energy	Protein
Elephant (1)	290.3 MJ (2)	2400 g (6.7 g per kg BW)
Human (3)	10.9 MJ	46 g (0.7 g per kg BW)

(1) Needs for an adult (37 years old), with a body weight (BW) of 3605 kg; elephants also practice geophagy to supplement Na, Ca, Mg and K and to detoxify plant compounds [94]; (2) 60 kg dry matter (1.65% BW, assuming 50% digestibility and 1790 kcal per kg); (3) Needs for an active adult male (2600 calories), 70 kg BW, assuming good-quality animal protein [95].

Despite the general lack of food in rainforests for people and elephants, there are some highly concentrated food sources that are profitable to exploit. These food sources, including elephant meat (for people), require some effort to obtain (Table 5). The following sub-sections of this paper examine the means in which forager communities and elephants in the Malay Peninsula deal with one another in accessing these resources.

Table 5. Alternative food returns for one day's effort for a family of foragers. (1) Gross energy (MJ) is the caloric value of the processed substance calculated using the USDA Food Composition Database <ndb.nal.usda.gov, 5 September 2018>, using "tapioca, pearl, dry" (cassava) for sago; "pork, fresh, loin, centre loin (chops), bone-in, separable lean and fat, cooked, broiled" for pig; "yam, raw" for yam; "honey"; "game meat, squirrel, cooked, roasted" for arboreal game; and "durian, raw or frozen". (2) Caloric yield (MJ) net of acquisition and processing costs (for one day with three adults spending six hours of effort each, plus their basal metabolic rate (BMR); i.e., 18 h of work and 72 h BMR = 32.7 MJ) and the thermic effect of food (estimated here at 10% of the gross caloric value). (3) We adjusted the figures that [4] give for *Elephas antiquus*, noting that they use fat-to-protein ratios based on the buffalo. (4) Refers to a moderately fat *Sus barbatus*. (5) Assuming 18 fruit @1.5 kg each; net caloric values for durian are negative assuming three person-days' foraging effort to obtain them; however, in practice, there is the option of camping next to the fruiting trees and incurring minimal effort, although this increases the risk of encountering elephants.

Food source	Gross MJ (1)	Nett MJ (2)	Protein	Ref.	Section
Elephant (3605 kg whole animal) (3)	9361	8392	283,738 g	[4]	Section 5.7
Sago (90 kg starch from 1 tree)	1314	1149	180 g	[96,97]	Section 5.2
Pig (50 kg meat from 1 animal) (4)	310	246	8195 g	[97]	Section 5.7
Yam (14.4 kg @ 0.8 kg per hr)	71	31	220 g	[53]	Section 5.3
Honey (4.2 kg)	53	15	13 g	[98,99]	Section 5.4
Arboreal game (7 kg)	51	13	2170 g	[53]	Section 5.7
Durian (27 kg fruit; 5.4 kg pulp) (5)	33	-3	79 g	–	Section 5.5

5.2. Dessert in the Green Desert: Carbohydrates from Palms

In terms of edible calories, wild palms (Arecaceae) are like oases in the green desert of the rainforest. Some communities, such as the Penan of Sarawak, successfully meet their caloric requirements by harvesting palms [97]. This section examines the partitioning of the 'palmivore' guild between people and elephants in the Malay Peninsula.

The most calorific product of forest palms is sago (locally known as *sagu*), which is the flour extracted from the stems of several monocarpic palms (Table 5). Sago is used in many food products internationally, and is boiled as a variant of tapioca (i.e., cassava) pudding. Although it has fallen out of use in some countries, sago remains a popular sweet dessert in others [100]. In Borneo, sago from *Metroxylon sagu* (native to New Guinea), is planted widely and is a staple food for many lowland communities. Sago from *Eugeissona utilis* (endemic to Borneo) has a stem that grows up to 15 m tall which is harvested from the wild by the hunter-gatherer Penans of the highlands of central Borneo, where no elephants are present [101]. The Penan harvest of sago is a form of para-cultivation, which involves managing the wild plants' production, while keeping them in their original environment [102]. In the Malay Peninsula, the Orang Asli derive a significant proportion of their calories from palms but do not regularly harvest sago. Endicott and Bellwood [53] found that the cabbage and pith of the sugar palm *Arenga westerhoutii* were one of the staple foods of the Bateks. Orang Asli also regularly eat palm fruit and kernels, and drink the sweet sap of the palm inflorescence [96]. The Orang Asli have even been found to eat palm beetles (*Rhyncophorus* spp.), both grubs and adults [96]. The cabbage palm, *Corypha utan*, found in the lowland swamps of the Peninsula, produces up to 90 kg of sago starch per palm, but it is not relied on by the Orang Asli [96]. The two species of *Eugeissona* that are native to the Peninsula (*E. brachystachys* and *E. tristis*) are both stemless, lacking the long trunk of Borneo's *E. utilis* [103]. The inflorescence of *E. tristis* (known as bertam in Malay) does contain a little sago which is occasionally eaten by the Orang Asli, [104] but the lack of a stem means that this species cannot be a significant supply of calories.

Several reasons have been put forward for the Orang Asli not relying on sago. Dentan [96] suggests that: (i) the riparian habitat of *C. utan* was replaced by rice paddies; (ii) there are adequate carbohydrates from trading forest produce for rice; and (iii) slave raiding against the Orang Asli made it too risky to live near the banks of the large rivers where *C.*

utan grows. Endicott and Bellwood [53], looking at the Bateks, rightly question whether there are in fact any suitable species of sago palm growing in their territories to begin with.

The threat of elephant depredation appears as another reason for the lack of an indigenous sago culture in the Peninsula. Unlike in central Borneo, the presence of elephants here means that sago palm cultivators have to contend with a significant source of depredation. Sago palms face occasional attacks from wild boar that are able to push over small palms, ripping them up with their tusks [96]. However, elephants can do much more damage to palm groves and are considered to be the only species of vertebrate that is a significant competitor for palms with human beings [36]. In addition to the loss of their crop, people put themselves at risk of elephant encounters if they camp close to such groves.

Asian elephants' preferred food are monocot plants, particularly grasses (e.g., [105,106]). During the Holocene, as the grasslands of the Malay Peninsula were replaced by forests, the populations of palms remained stable [21]. Thus, the ability to exploit palms may have proved crucial for the survival of elephants. Olivier [36] emphasised that elephants are uniquely pre-adapted to overcome the physical defences of palms, "being capable of intelligently combining the use of its size, strength, toenails, tusks, and particularly the manipulative abilities of its trunk". He added that the ability to exploit a palm niche is so unique that he proposes the term "palmivory" as distinct from other forms of herbivory, such as browsing and grazing. In the forests of the Malay Peninsula, palms may be the main source of carbohydrates for elephants. Olivier [36] noted that elephants eat most species of palms, including all the sago palms *M. sagu*, *E. tristis*, and *C. utan*. Indeed, elephant palmivory likely contributed to the short stature, limited diversity, and restricted distribution of native sago palms in the Peninsula. Terborgh et al. [37] found significantly higher numbers of palms in a forest where elephants had been recently removed (~20 years earlier), compared with a forest where elephants still lived; in particular, large palms (>1 m tall) were eight times more abundant in the forest without elephants.

In contrast to the Peninsula, the relative scarcity of elephants in Borneo may be the reason for the relative abundance and subsequent para-cultivation of tall-stemmed sago palms on the island. In particular, the absence of elephants in the highlands of Borneo seems to have allowed the evolution of the Penan sago culture associated with the tall-stemmed *Eugeissona* palms.

In conclusion, we suggest that the prehistoric and continued presence of elephants is the main reason that reliance on sago is not an option for the foragers of the rainforests of the Malay Peninsula. Palms do provide a source of food, but it is a source that is effectively exploited by elephants. In elephant landscapes, palms alone are thus seldom able to provide groups of people with enough calories for subsistence.

5.3. A Proboscidean Perspective on the Wild Yam Problem

Instead of sago, it is root crops that provide the main source of carbohydrates for foragers of the Malay Peninsula [52,96]. Early studies suggested that wild yams were too scarce as to be relied upon without recourse to cultivated food [49,83,90,107]. However, Endicott and Bellwood [53] highlighted archaeological evidence that showed human occupation of caves deep in the forested interior of the Peninsula, suggesting that independent rainforest subsistence may have been possible. This evidence prompted Bailey and Headland [91] to suggest that: "humans have subsisted in tropical rainforest independently of cultivated foods only in [Peninsular] Malaysia". In this section we examine how people gained an edge over elephants to allow them to exploit wild yams. The Peninsula is home to roughly 20 native species of yam in the genus *Dioscorea* [103]. Batek yam para-cultivation involves replanting the heads of wild tubers and returning to harvest them [52]. In addition, the cultivation of introduced species of root crops has probably been taking place in the Malay Peninsula for more than 10,000 years [66]. The four main species of tubers (belonging to four different families) cultivated here are taro (*Colocasia esculenta*, Araceae), purple yam (*Dioscorea alata*, Dioscoreaceae), sweet potato (*Ipomoea batatas*, Convovulaceae), and cassava (*Manihot esculenta*, Euphorbiaceae). All of them were introduced, but some were probably domesticated in the region, or in New Guinea, during the Pleistocene or early Holocene [108].

Elephants, like people, also eat forest tubers. As with para-cultivation by people, yam digging by elephants may actually be of some benefit to the plant if it results in propagating parts of the tuber. In the Congo, African forest elephants compete with people for the largest forest yam, known as 'Bà' (*Dioscorea mangenotiana*) [109,110]. Dounias [102] noted that elephants are the "only [non-human] mammal capable of removing the heavy yam head". In the Malay Peninsula, elephants eat all four species of cultivated tubers but Olivier's [36] elephant food list does not include observations of any of the wild species. Other studies on the diet of Asian elephants also do not mention wild tubers [106,111,112]. L. Ong (pers. comm., 5 August 2018) observed elephants feeding in Pahang and found that elephants do frequently uproot plants to eat, but she did not observe wild *Dioscorea* spp. in her study site. Separately, interviews of Jahai and Temiar individuals in Belum-Temengor found that they did not report *Dioscorea* spp. among the plants eaten by elephants.

People have two advantages over Asian elephants when it comes to exploiting wild yams: excavation and detoxification. People with digging sticks are well able to locate and excavate tubers, whereas Asian elephants face some challenges. African elephants are well adapted to digging up yams, with both males and females having tusks. Among Asian elephants, only males have tusks, and not all males [113]. Tuskless elephants can still dig using their feet but this is likely to be less effective. In addition, tubers in Asia are generally smaller and more scattered than the giant African species.

Perhaps most significantly, some Asian species of *Dioscorea* (e.g., *D. prazeri* and *D. hispida;* Figure 3) possess toxins (cyanic acid and the alkaloid dioscorine). Toxins are not completely effective against elephants, who are able to consume such compounds because their large guts contain significantly more bacterial and protozoan symbionts that detoxify plant defences [114]. Elephants also regularly practice geophagy to neutralise plant toxins [115,116]. Nevertheless, detoxification imposes a cost on elephants, and thus they prefer eating non-toxic plants such as grasses and palms [36].

(**a**) (**b**)

Figure 3. (**a**) Batek woman digging the tubers known as *takop* (*Dioscorea orbiculata*); (**b**) harvested tuber fragments. *Source*: (**a**) Endicott, K. M. (1976). Woman digging tubers. Keene State College Orang Asli Archive, Kirk & Karen Endicott Collection, accessed on 4 November 2021, reproduced with permission; (**b**) Wong Pui May (2018), reproduced with permission.

The Menraq also practice a degree of geophagy (e.g., [117]). In addition, they know how to process and cook yams safely [53,96]. Indeed, evidence from the Niah caves in Sarawak suggests that people in Southeast Asia have had the ability to detoxify poisonous plants (including *D. hispida* and the poisonous nut *Pangium edule*) for at least

40,000 years [108]. Due to their digging tools and their ability to process and cooking yams, people in the Peninsula may thus be better adapted than Asian elephants at exploiting the wild yam niche.

5.4. Honey Hunters

In addition to the gradients of altitude, latitude, and seral succession, the abundance and quality of some food resources may increase as one moves from the forest floor up through the canopy of primary rainforest [118]. By hunting with blowpipes and climbing trees, humans manage to access resources that are not available to ground-dwelling animals [21,119]. In this section we consider a particular arboreal trophic resource that is available to people and not normally to elephants: honey from bee hives.

In addition to complex carbohydrates and animal fat, simple sugars can also be an important source of calories [96]. In the Malay Peninsula, honey from several bee species, including *Apis dorsata*, can be a particularly important source of sugar calories for Menraq groups such as the Bateks, who climb up to 50 m into the canopy to access it [48,52,99,120]. In pursuing this resource, the people of the Malay Peninsula have long had a "social partnership" with honey guides (*Indicator archipelagicus*), while they compete with honey buzzards (*Pernis ptilorhynchus*) and sun bears (*Helarctos malayanus*) [121]. Indeed, human remains from the time of the Hoabinhian (10,000–2000 BCE) show signs of dental caries, leading Bulbeck [122] to suggest that the prehistoric ancestors of the Orang Asli had a diet rich in fruit and honey.

Elephants also have a sweet tooth and eat honey if they can get it. In Africa, Estienne and Boesch [123] note how forest elephants prey on the grubs and honey of ground-dwelling Melipone bees (*Meliplebeia lendliana*). However, in the Peninsula, the hives of bees such as *A. dorsata* are usually out of reach of elephants, and even the lower-nesting *A. florea* are probably not attractive due to the aggressive stinging behaviour of *Apis* bees, which King et al. [124] have shown to be a deterrent of elephants in Sri Lanka. By comparison, there is a genus of stingless bees (*Trigona* spp.) that are found in crevices that are often low enough for elephants to reach, and we found that in Belum-Temengor the elephants attack the hives and eat the honey of these stingless bees when the opportunity arises [64].

5.5. Fruit Gardeners

The other sweet resource of Malaysia's rainforest canopies comes from the abundant fruiting of several tree species. These include the durian *Durio* spp. (Bombacaceae) (Figure 4, below), mango *Mangifera* spp. (Anacardiaceae), and rambutan *Nephelium lappaceum* (Sapindaceae). Both humans and elephants belong to the trophic sub-guild of forest-floor frugivores. During the irregular periods of fruit availability of the Malay Peninsula, both humans and elephants exploit the abundance of fruit on the forest floor. Elephants access fruit when it falls to the forest floor, when they can reach it on the tree, and when they can shake it out of the tree [66,125,126]. In Perak, a Temiar villager reported that an elephant had pushed over a rambutan tree full of fruit [64]. This section examines the strategies people of Malaysia take to avoid conflict with elephants for fruit, focusing on durians, the most calorific fruit (Table 5) and a favourite of both people and elephants.

Due to their large fruits, thick husks, and sharp prickly thorns, durians are inaccessible to many forest animals and must have relied largely on elephants (and probably bears; pers. obs.) for seed dispersal [127,128], at least before the arrival of humans. The durian's strong smell attracts many creatures, but elephants have an exceptionally good sense of smell [129], can remember the location of fruit trees [93,130], and can easily split open durians by stepping on them (pers. obs.). Corner [131] described how elephants' dominance in terms of size means that they have first choice of the fallen durian fruit, before "tigers, pigs, deer, tapir, rhinoceros, monkeys, squirrels, and so on down to ants and beetles". In addition, their social flexibility means that, during the fruit season, groups of elephants as large as 60 individuals can congregate together around the fruiting trees [36,132]. Corner [131] described the floor of a fruiting durian grove as follows: "Under the big trees are leaning saplings, frayed bark, trampled shrubs, and churned ground, as scenes of elephantine supremacy."

Figure 4. Durians (*Durio* spp.) are sought-after by both elephants and people. Credit: T. Lim/MEME 2016.

The Menraq are also fond of durian and are similarly well placed to exploit it. Although not on par with elephants, the Menraq have exceptional olfactory abilities [133], good orienteering ability [134], and can easily open a durian by splitting it along its seams using a blade (pers. obs.). Like elephants, humans also have social flexibility, and the size of a Menraq camp may increase during the fruiting season—the unity of a camp being based solely on the "moral obligation each family has to share food with all other families in the camp" [53]. Unlike elephants, the Menraq climb and collect unripe durians from high up in the trees [48]. The Menraq also build above-the-ground shelters next to fruiting trees so when they hear a fruit fall they can climb down, grab it, and then climb again to eat it in safety. This approach does not always work and one early account noted that elephants had managed to tear down platforms as high as 6 m above the ground [79]. Another strategy for reducing conflict over durian fruit is to ensure that durian trees are spread out widely enough that both elephants and people can access them without encountering one another. Over the millennia, human campsites were often deliberately enriched and were planted as *dusun*—orchards or agro-forestry fruit gardens. Moore et al. [135] found that fruit gardens in Krau Wildlife Reserve, in the centre of the Peninsula, contained five times as many fruit-producing trees as the surrounding forest. John Terborgh (pers. com.) suggests that, compared to monocultures, these mixed plantations are less vulnerable to elephant depredation. In the forest of Temengor, on the route to Kg. Lengweg [136], we noticed that the Temiars had planted durian trees—both *D. zibethinus* and a forest durian species (Figure 4)—at intervals of at least 500 m apart. One of the benefits of this planting strategy would be to reduce the ability of elephants to dominate the entire durian crop and thus ensure that people had a chance to also get their fill.

5.6. Swidden Farming: Elephants in the Fallow Field

During the Pleistocene, foraging human communities and elephants may have established a way of life that avoided encounters with one another. More recently, several changes have taken place that have altered the dynamics of the interactions. In particular, the advent of agriculture during the Neolithic period (around 5000 years ago in the Malay Peninsula) had important impacts on both humans and elephants. In the lowlands of the Malay Peninsula the Menraq continued to practice a lifestyle based primarily on foraging—with depredation by wild animals (particularly wild boar) said to be one of the main reasons why they do not plant crops [48]. In contrast, a group of Orang Asli in the highlands of the centre of the Peninsula (the Senoi) commenced swidden farming of crops such as rice, millet, and bananas [49].

Swiddening involves cutting down a patch of canopy trees to create a clearing which is burned and then planted for a few years. The secondary forest that grows back after a swidden is left fallow, and contains grasses and herbs which can be eaten by herbivores such as elephants [41,84,137]. This development had a mixed impact on elephants. Although it made more food plants available (both crop and fallow), it also increased the number of “dangerous” humans, increasing the potential for conflict. On balance, several findings from around the world suggest that, in contrast to settled agriculture (including plantations), swiddening can actually be compatible with elephant conservation. The one location in China where elephants survived was in the south, where the local Dai people practiced swidden farming [14,29]. Similarly, in India, Sukumar [138] finds that shifting cultivation, practiced on a small scale (i.e., still maintaining significant forest cover), does not damage elephant habitat. Furthermore, in Sri Lanka, traditional “chena” swiddening has been shown to be compatible with elephant conservation [139,140]. In the Peninsula, Olivier [36] found that the fallow swiddens (known as “belukar” in Malay) contained 36% more trunkfuls of elephant food plants (trees, palms, herbs, bamboos, and grasses), and thus supported significantly more elephants compared with primary forest. Olivier [36] noted that the reliance of elephants on human swiddens meant that they may perhaps be thought of as “having entered a sort of commensal relationship with man”.

5.7. Predation: Calories from Animal Protein

As omnivores, humans have an advantage over elephants in our ability to catch and consume animal fat and protein. Animal fat is a known substitute for starches as a source of energy in periods of scarcity [90] and, although an over-reliance on lean meat can be unhealthy, in normal circumstances, humans can also rely on protein for up to 35% of our total caloric needs without ill effect [4,141,142]. Hunting is therefore an additional means by which humans can overcome the caloric deficit of environments where carbohydrates are scarce. Moreover, humans can also hunt elephants directly.

Predation is a key selective pressure on prey animals and the introduction of a predator species can cause substantial differences in the prey population’s morphology, physiology, and behaviour [143]. Although tigers may occasionally attack young elephants [144], adult Asian elephants have no natural predators. This changed with the arrival of modern humans [3].

Human hunting had varying impacts on elephant populations throughout Asia. In Sri Lanka, millennia of selective hunting of tuskers have led to a current population where only about 3% of male elephants have tusks [113]. In the Malay Peninsula, there is little archaeological evidence of elephants being hunted [145], and at present most males have tusks (pers. obs.). It is possible that hunting played a role in the extinction of other proboscidean species in the region, although the evidence points to the loss of grasslands due to climate change as the primary cause [40]. There is a single record of *Stegodon* from the Peninsula: a late-Pleistocene tooth of a juvenile found in a cave in Perak [146].

There are very few references of the Menraq hunting large game such as elephants, banteng (*Bos javanicus*), or seladang (gaur, *B. gaurus*) [41,48,52,147]. In the early 20th century, the Menraq abandoned the use of bows and arrows and now hunt mainly by blowpipe [148].

Endicott [48], who studied the Bateks, characterised the fact that they seldom hunt or trap large game as a "mystery"; indeed, it is remarkable that they do not use traps for any type of game. Possible reasons that have been put forward for them not hunting pigs and large game relate to questions of practicality, to the risk of injury, and to personal preferences [48].

Another factor regarding the Menraq not hunting large game is the fact that the numbers of such animals are relatively low in the rainforest. Large game is found at very low densities in primary rainforest. For example, the large bovids such as banteng occur at 10–15 animals per km^2 in semi-arid forests but in primary rainforest are usually no more than 1–2 per km^2 [149], and in the Peninsula were seldom found south of the Kangar-Pattani line ($6°26'$ N) [137]. The seladang is found more widely in the Peninsula, but its presence is thought to be largely dependent on the opening up of the forest by swidden farmers [137].

Despite the low density of large game in the primary rainforest, there is a significant volume of other forms of animal protein in this environment. Dentan [84,96] pointed out that the Orang Asli opportunistically forage on "lots of little things", including insects, lizards, tiny fish, and snails. Similarly, Endicott [48] also found that blowpipe hunting of arboreal animals (primates, squirrels, birds), and the hunting method that he describes as "getting animals out of holes" yields an adequate supply of mammal, reptile, and bird meat over the long run (147 g of meat or 30 g of protein per person per day)—supplemented by vegetable protein. Protein from fish can play a particularly important source of calories of forest foragers during periods of scarcity when the fat stores of other prey animals are depleted [150].

In summary, it is probable that one additional reason why the Menraq seldom hunt elephants is that there is a significant risk associated with antagonising the local elephant population. Nonetheless, both swiddener and settler farming communities occasionally hunt elephants.

6. Conclusions

The results of this review suggest that, in several key respects, elephants and people in the rainforests of the Malay Peninsula have managed to partition their respective ecological niches to enable them to coexist. In particular, the indigenous people focused foraging efforts on yams and arboreal food resources that are inaccessible or undesirable to elephants (and tigers); and the grasses and leaves eaten by elephants were of little importance to these people (Table 2). These dynamics were upset by the advent of swidden farming and plantation agriculture such as oil palm and rubber. This finding has several implications for the conservation of elephants and of biodiversity more generally.

The strength of the narrative, interpretation, and commentary that we provided in this paper is observational and anecdotal rather than experimental. Indeed, one reason the study of ecological relationships between people and elephants has received relatively little attention by ecologists is because it does not lend itself well to experimentation. The large-scale and long-term nature of human–elephant interactions makes it difficult to design a rigorous and empirical basis upon which to gather evidence to test such complex ecological hypotheses.

A related issue is that fact that the absence of experimental or archaeological data leads to a reliance on ethnographic analogy to illuminate the prehistoric relationship between humans and elephants. We acknowledge that such analogy is one of the most controversial areas of theoretical archaeology [151,152], and that there are likely significant differences between the contexts and cultures of the Tampanian, the Hoabinhian, the historical Orang Asli, and the Orang Asli today. Furthermore, we trust that it is clear that the cultural practices that we describe in this paper, such as not hunting pigs, have not applied consistently throughout history, and by no means apply to all Orang Asli today. Indeed, the taboo against pig hunting does not apply to all Menraq, or even to all Bateks. Such practices are even variable within a single community: for example, one Jahai village that we visited had only stopped hunting pigs a few years prior to our visit, and although it appeared to us that the whole village respected the taboo, the reasons for this shift were far from clear. Such dynamic and varied beliefs prevent broad generalisations about culture [153] but they do not subtract from the value of the cases as illustrations of examples of the central point of this paper: the flexibility of our fundamental niche which can, whether consciously or not, enable coexistence with megafauna.

One important aspect of conserving elephants in the Peninsula is the nature of official programs that encourage (and often coerce) the Orang Asli to adopt a "modern" and "civilized" lifestyle. These programs often overlook the adaptive aspects of the traditional lifestyles of the Orang Asli with respect to sharing a landscape with large mammals such as elephants and tigers. Many aspects of Menraq culture that are viewed by the authorities as "primitive", can actually be explained as being adaptations to the practical realities of life in the rainforest, particularly to living in a landscape influenced if not dominated by dangerous megafauna such as elephants and tigers. For example, Roseman [154] notes that some urbanites take a culturalist position and negatively characterise the Orang Asli as "people who live in trees", failing to grasp the selective advantage of arboreal retreats when living in the rainforest. Such derogatory attitudes often extend to many other aspects of the Orang Asli's traditional rural culture.

From the perspective of elephant conservation, the key aspect of traditional cultures is their relatively low population density. The "development" resulting from the fossil-fuel economy of the latter half of the 20th century resulted in a dramatic increase in the population of the Malay Peninsula, including the population of the Orang Asli. This increase often results in a "landscape of fear" [155] that effectively excludes elephants. Furthermore, permanent settlement, adoption of a cash-based economy, and a reliance on plantation agriculture results in increased competition and conflict. These trends can reduce tolerance of elephants via a process of "othering", whereby elephants are marked as "different" and unwelcome [156]. This is an example of the more general tendency of modernity to break traditional attitudes of respect towards animals (as other-than-human-persons) and towards the natural world as a whole [157].

In summary, there is evidence that, in the rainforests of the Malay Peninsula, elephants and humans succeeded in somewhat partitioning their spatial, trophic, and temporal niche. People managed to avoid elephants by climbing trees at night; similarly, elephants managed to avoid people by retreating to the forest during the day. People found sustenance via yams, arboreal food (fruits and game), and honey, which are largely inaccessible to elephants. It is clear that the presence of large mammals such as elephants and tigers had a significant influence on the culture and lifestyles of forest people and the presence of people had a similar influence on the behaviour of elephants. Lessons for conservation include the need to recognise that the adoption of settled lifestyles, particularly plantation agriculture, destabilise these established relationships and thus could reduce humans' and elephants' tolerance of one another. Furthermore, the long-term survival of wild elephants in Southeast Asia will require further adjustments from both species to coexist under the novel conditions of the Anthropocene. In addition to occupying protected area refugia, elephants will need to learn to roam and feed in highly fragmented and developed landscapes without exceeding people's tolerance for crop raiding and safety risk. Similarly, people, in addition to preventing illegal elephant killing for ivory and other body parts, will need to accommodate elephant behavioural and ecological needs (e.g., [158,159]) in our landscape development models and increase tolerance to the risks involved in sharing landscapes with the largest terrestrial animals on Earth.

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