



Foraging impacts of Asian megafauna on tropical rain forest structure and biodiversity

John Terborgh^{1,2}, Lisa C. Davenport², Lisa Ong³, and Ahimsa Campos-Arceiz^{3,4,5} 

¹ Center for Tropical Conservation, Nicholas School of the Environment and Earth Sciences, Duke University, PO. Box 90381, Durham, NC 27708-0831, USA

² Florida Museum of Natural History and Department of Biology, University of Florida, Gainesville, FL 32611, USA

³ School of Environmental and Geographical Sciences, The University of Nottingham Malaysia Campus, Jalan Broga, 43500 Kajang, Malaysia

⁴ Mindset Interdisciplinary Centre for Environmental Studies, The University of Nottingham Malaysia Campus, Jalan Broga, 43500 Kajang, Selangor, Malaysia

ABSTRACT

Megaherbivores are known to influence the structure, composition, and diversity of vegetation. In Central Africa, forest elephants act as ecological filters by breaking tree saplings and stripping them of foliage. Much less is known about impacts of megafauna on Southeast Asian rain forests. Here, we ask whether herbivory by Asian megafauna has impacts analogous to those of African forest elephants. To answer this, we studied forest (1) structure, (2) composition, (3) diversity, and (4) tree scars in Belum and Krau, two protected areas of Peninsular Malaysia, and compared the results with those obtained in African forests. Elephants are abundant in Belum but have been absent in Krau since 1993. We found that stem density and diversity, especially of tree saplings, were higher in Krau than in Belum. Palms and other monocots were also more abundant in Krau. In Belum, however, small monocots (<1 m tall) were very abundant but larger ones (>1 m tall) were virtually absent, suggesting size-selective removal. The frequency of stem-break scars was equal at Belum and Krau but less than in Central Africa and greater than in the Peruvian Amazon where tapirs are the only megafauna. Pigs and tapirs could also contribute to the high frequency of tree scars recorded in Malaysian forests. Forest-dwelling elephants in Asia seem to have a reduced impact on tree saplings compared to African forest elephants, but a very strong impact on monocots.

Abstract in Malay is available with online material.

Key words: Defaunation; ecosystem function; *Elephas maximus*; forest dynamics; herbivory; *Loxodonta cyclotis*; Malaysia; megafauna.

THERE IS SUBSTANTIAL LITERATURE ON THE FORAGING OF ELEPHANTS, nearly all of it focused on dry woodlands and savannas. In these environments, elephants, both Asian (*Elephas maximus*) and African (*Loxodonta* spp.), have huge impacts on the structure, composition, and diversity of vegetation, and in some contexts can drive alternative states, *i.e.*, dense woodland (vs.) open savanna (Owen-Smith 1988, Sukumar 2003, Skarpe *et al.* 2004, Rutina *et al.* 2005). In contrast, little is known about the impacts of elephant foraging in closed canopy evergreen forests in Africa (Short 1981, White *et al.* 1993) and even less in Asia.

Elephant browsing in savanna environments is well-known to result in landscape-scale changes, including selective reduction in favored species, reduced tree density, promotion of bushy (vs.) upright morphology and reduced species diversity (Kerley & Landman 2006, Asner *et al.* 2009). But what are the impacts of elephants in closed-canopy forests where dense vegetation largely precludes direct observation? Assessments of elephant foraging in forests have been based on indirect methods, including

microhistology of plant fibers and carbon isotope analysis of dung, identification of feeding signs in plants, and observation of captive elephants feeding in natural vegetation environments (Struhsaker *et al.* 1996, Chen *et al.* 2006, Himmelsbach *et al.* 2006, English *et al.* 2014, Yamamoto-Ebina *et al.* 2016). These analyses have shown that forest-dwelling elephants consume a broad range of dicots and monocots, both in Africa and Asia (Merwe *et al.* 1988, Tieszen *et al.* 1989, Sukumar & Ramesh 1995, Steinheim *et al.* 2005, Chen *et al.* 2006, Himmelsbach *et al.* 2006, English *et al.* 2014, Yamamoto-Ebina *et al.* 2016).

As background, we first review results obtained with African forest elephants (*L. cyclotis*) in previously published research (Terborgh *et al.* 2016a,b). We compared sites in Gabon with zero, low, medium, and high elephant densities. The density of small saplings (≥ 1 m tall, <1.0 cm dbh) and the diversity of both small and large (≥ 1.0 cm dbh, <10 cm dbh) saplings was significantly greater at sites with few or no elephants than at sites where there were many. In the tall forests of Central Africa, forest elephants forage on trees by breaking and stripping saplings >2.0 cm and <6.0 cm in diameter (Struhsaker *et al.* 1996, Scheil & Salim 2004). Many of these re-sprout and continue growing, leaving a prominent scar at the break point. Saplings in this diameter range

Received 9 June 2017; revision accepted 19 July 2017.

⁵Corresponding author; e-mail: ahimsa@camposarceiz.com

at protected sites supporting unpoached elephant populations in Gabon carried break scars at the rate of 107 per 100 stems (some stems showed two, or even three breaks) (vs.) 31 per 100 stems in Peru, where megafauna is largely lacking. What we referred to as ‘background breaks’ (Peru) are presumptively caused by falling debris and crown dieback and would occur also in the presence of megafauna. The higher number of breaks observed in Gabon ($107 - 31 = 76$ per 100 stems) was attributed to elephant foraging (Terborgh *et al.* 2016b).

Here, we ask whether the foraging of elephants (and possibly other large herbivores) in closed canopy Southeast Asian forests results in impacts analogous to those documented in Gabon. We attempt to provide a preliminary answer to this question through comparing the structure and diversity of understory vegetation at two sites in Peninsular Malaysia, one with a high but not quantified density of elephants (Royal Belum State Park) and one without elephants (Krau Wildlife Reserve, Fig. S1). Specifically, we investigate whether there are differences between both sites in (i) stem density of different plant types (dicots [vs.] monocots, and lianas [vs.] trees) and age classes (seedlings, saplings, and adults); (ii) diversity of the above plant types; and, (iii) frequency and height distribution of break scars in dicot tree saplings. These results are then compared with data from Gabon.

Belum and Krau differ in latitude by 2 degrees (~ 5.5 N [vs.] ~ 3.5 N respectively). The difference is small, but there is a well-documented drop in tree diversity north of the Kangar-Pattani Line, a biogeographic transition for plants that runs west-east around 7° N near the border between Malaysia and Thailand (e.g. Woodruff 2003 and references therein). Both of our sites lie well south of the Kangar-Pattani line. There are also small, but possibly relevant differences between the sites in climate and soils that could have influenced our results. The results presented should therefore be considered as preliminary.

METHODS

STUDY SITES.—We conducted this study in two protected areas of Peninsular Malaysia – the Royal Belum State Park (Belum), a forest with elephants, and Krau Wildlife Reserve (Krau), a forest without elephants since 1993 (Fig. S1). Belum ($5^\circ 35'$ N, $101^\circ 20'$ E) is the second largest protected area in Peninsular Malaysia (1175 km^2) and is part of a much larger block of continuous forests that extends into Southern Thailand. It is a hilly area with an altitudinal range of ~ 260 – 1500 m above sea level and vegetation that includes lowland dipterocarp, hill dipterocarp, and montane forests. Much of Belum is submerged under Tasik Temengor, a large man-made lake dammed in the late 1970s. Belum was gazetted in 2007 and (most of it) has never been logged. It is rich in biodiversity, including over 3000 species of flowering plants, 185 bird species, and a wide range of endangered mammals including Asian elephants, tigers (*Panthera tigris jacksonii*), gaurs (*Bos gaurus*), and Malayan tapirs (*Tapirus indicus*). Some large mammals such as Javan (*Rhinoceros sondaicus*) and Sumatran (*Dicerorhinus sumatrensis*) rhinos, and bantengs (*Bos javanicus*) became locally extinct in the past few decades. Judging from abundant sign,

Asian elephants are plentiful, although there is no quantitative information on their density in the landscape.

Krau ($3^\circ 24'$ N, $101^\circ 28'$ E) is smaller (600 km^2), with an altitudinal range of 45–2108 m above sea level. Like Belum, Krau has not been commercially logged and its vegetation consists predominantly of lowland dipterocarp forest, hill dipterocarp forest, and upper dipterocarp forest. Krau is isolated from other large forest patches, being surrounded by highly fragmented forests and rubber and oil palm plantations (Fig. S1). In recent decades, Krau has also lost its rhino and banteng populations; unlike Belum, Krau has had no wild elephants since 1993 when the last resident herd was captured and translocated to a larger forest by the local authorities. Tigers and gaurs are ecologically extinct in Krau, being virtually extirpated. Neither in Belum nor Krau there is any reliable estimate of tapir and wild pig (*Sus scrofa*) densities. All measurements at both sites were conducted in primary lowland dipterocarp forest.

VEGETATION SAMPLING.—As other investigators have done (e.g., Merwe *et al.* 1988, Chen *et al.* 2006), we used an indirect method to study megafaunal foraging impacts, sampling plants rather than dung and comparing sites with and without elephants. For comparative purposes, we applied the same vegetation sampling methodology as previously employed in Gabon and Perú (Terborgh *et al.* 2016a,b).

We marked, measured and identified all stems ≥ 1 m tall within 100 m^2 strips (rectangular plots of 5×20 m), of which we completed 7 at both Royal Belum and Krau. The strips provided samples of 75 – 250 saplings, including both small (≥ 1 m tall, < 1 cm dbh) and large (≥ 1 cm dbh, < 10 cm dbh) saplings, but few trees. The strips were then subsampled for stems < 1 m tall in two 2×2 m ($= 4 \text{ m}^2$) squares situated in the SW and NE corners of each strip, for a total of 8 m^2 per strip. Stems were further characterized as dicots (trees or lianas) and monocots (palm, bamboo, cyperaceae, ginger, pandan, and others).

At each sampling station, we evaluated stems ≥ 2 cm dbh, < 6 cm dbh (in the vicinity of but not within the formal 100 m^2 plots) for past breaks within arbitrarily oriented 2 m wide transects that were continued until a tally of 100 stems was achieved or exceeded. The goal here was to discriminate the frequency and height distribution of breaks attributable to megafaunal herbivory. Doing this required subtracting the height distribution of background breaks from the observed distribution of breaks at sites with megafauna, as in Terborgh *et al.* (2016b). Background data on stem breaks was obtained in the Peruvian Amazon where tapirs (*Tapirus terrestris*) comprise the only megafauna (details in Terborgh *et al.* 2016b).

All sampled stems were identified in the field by *orang asli* collaborators. The *orang asli* are indigenous people native to the Malay Peninsula. The *orang asli* we worked with possessed a comprehensive knowledge of the botany in their respective districts. We recorded phonetic approximations of the *orang asli* names for each stem and collected corresponding samples. Later, we spread out all the specimens from each strip and sorted them into morphospecies. We found that the names given to us by the *orang asli*

almost perfectly corresponded to our morphospecies with an agreement of around 98%. We thus used the *orang asli* determinations as the basis of our reported diversity estimates.

DATA ANALYSIS.—All statistical analyses were conducted using R statistical environment (v. 3.2.4; R Core Team, 2016). We used two-sample *t*-tests to analyze site differences (Krau [vs.] Belum) in the density of stems of different plant categories and the height distribution of stem breaks in dicot saplings. We calculated Fisher's alpha values on morphospecies designations separated by size classes using the function *fisher.alpha* in R's *vegan* package (Oksanen *et al.* 2015).

RESULTS

We found no difference between Belum and Krau in the overall density of the smallest class of stems, those <1 m tall (22.1 ± 19.8 per m^2 in Krau (vs.) 16.8 ± 13.0 in Belum; $t = -1.65$, $df = 94.943$, $P = 0.102$). However, there were pronounced differences between the two sites in the density of stems ≥ 1 m tall, Krau having nearly double the density ($204.7 \pm 27.5/100 m^2$) of Belum ($103.9 \pm 39.9/100 m^2$; $t = 5.5$, $df=10.6$, $P = 0.0002$). Densities of both small (≥ 1 m tall, <1 cm dbh; 110.6 ± 30.5 (vs.) 50.6 ± 28.3 stems per $100 m^2$; $t = -5.4$, $df = 10.55$, $P = 0.0003$) and large (≥ 1 cm, <10 cm dbh; 66.3 ± 18.4 [vs.] 42.1 ± 20.2 stems per $100 m^2$; $t = -2.3$, $df = 11.9$, $P = 0.038$) tree saplings were higher at Krau (Fig. 1). Lianas constituted a small portion of stems at both sites (Fig. 1). Small liana saplings were marginally denser in Krau ($19.9 \pm 17.6/100 m^2$) than in Belum ($5.3 \pm 4.6/100 m^2$; $t = -2.13$, $df=6.8$, $P = 0.072$), while the numbers of large liana saplings did not differ between sites (4.7 ± 5.1 [vs.] $3.0 \pm 2.8/100 m^2$; $t = -0.79$, $df=9.3$, $P = 0.45$; Fig. 1).

When the monocot component of these data is analyzed separately, a strong contrast emerges (Fig. 2). Palms were more abundant at Krau than at Belum – small palms (<1 m tall) were three times more abundant (39 [vs.] 13 stems per $100 m^2$;

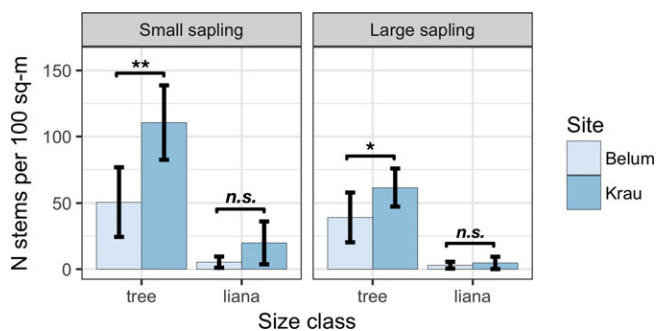


FIGURE 1. Density of small (≥ 1 m tall, <1.0 cm dbh) and large (≥ 1 cm dbh, <10 cm dbh) saplings at Belum and Krau. Data for trees and lianas are separate. Error bars indicate 95% CI. Asterisks and annotations indicate significance levels of statistical comparisons: *n.s.*, not significant (*i.e.*, $P > 0.05$); * $P < 0.05$; ** $P < 0.01$.

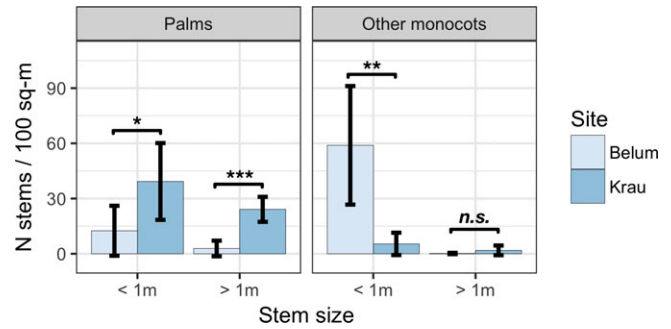


FIGURE 2. Density of non-palm monocots and palms <1 m tall and >1 m tall at Belum and Krau. Error bars indicate 95% CI. Asterisks and annotations indicate significance levels of statistical comparisons: *n.s.*, not significant (*i.e.*, $P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

$t = -2.2$, $df = 94.5$, $P = 0.034$) and large palms (>1 m tall) eight times more abundant (24.1 [vs.] 2.9 stems per $100 m^2$; $t = -6.5$, $df = 10.1$, $P \ll 0.001$). Small (<1 m tall) non-palm monocots (bamboo, gingers, pandans, Cyperaceae) were 12 times more abundant at Belum (59 [vs.] 5 stems per $100 m^2$; $t = 3.3$, $df = 58.9$, $P = 0.002$), while the larger ones (>1 m tall) were similarly rare in both sites (0.15 [vs.] 1.9 stems per $100 m^2$; $t = -1.5$, $df = 6.2$, $P = 0.16$; Table 1 & Fig. 2).

Indirect evidence of megafaunal foraging can be obtained from assessing the frequency and height of break scars on saplings ≥ 2 cm, <6 cm dbh (Terborgh *et al.* 2016b). The number of breaks per 100 stems did not differ between the two sites, being 72.1 ± 92.6 at Belum and 73.7 ± 75.6 at Krau ($t = -0.15$, $df = 201.4$, $P = 0.88$), values intermediate between those obtained in Gabon (107) and Peru (31). The distributions of break heights were quite different between Belum (mean= 1.05 ± 0.82 m) and Krau (1.58 ± 0.82 m; $t = -4.36$, $df = 180.7$, $P < 0.001$). More than 2/3 of the breaks at Belum were below 1 m whereas only 28% were at Krau. Fig. 3 presents the normalized height distributions of breaks at Belum, Krau, and Gabon after subtraction of background breaks, as recorded in the Peruvian Amazon. The pattern of breaks in Krau resembled that at sites with high densities of elephants in Gabon (Fig. 3).

Finally, we compared the mean diversity (Fisher's alpha) of small and large saplings at Belum and Krau with those found in Peru and Gabon (Fig. 4). Sapling diversity at Krau (Fisher's alpha ca 100) was more than twice that at Belum (ca 35), both for small

TABLE 1. Taxonomic break-down of 2164 saplings (≥ 1 m tall, <10 cm dbh) registered in $14 \times 100 m^2$ strips, 7 at Belum and 7 at Krau.

Class	Dicot		Monocot					Total
	Tree	Liana	Palm	Bamboo	Cyper	Ginger	Pandan	
Krau	1072	205	151	4	3	1	1	1437
Belum	649	75	2	0	0	0	1	727
Total	1721	280	153	4	3	1	2	2164

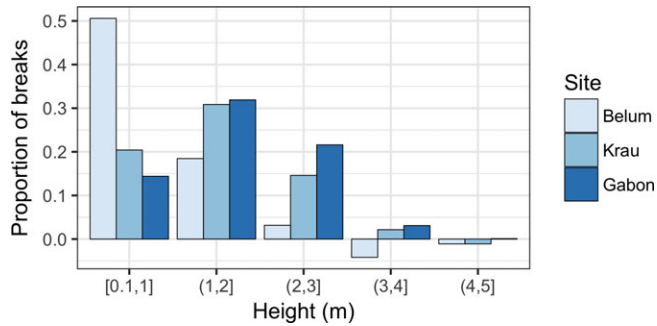


FIGURE 3. Height distribution of excess stem breaks attributable to elephants foraging at Belum, Krau, and Gabon after removal of background breaks attributable to other causes (34.4 breaks/100 stems, pro-rated by heights, based on breaks at Casa Machi, Peru)

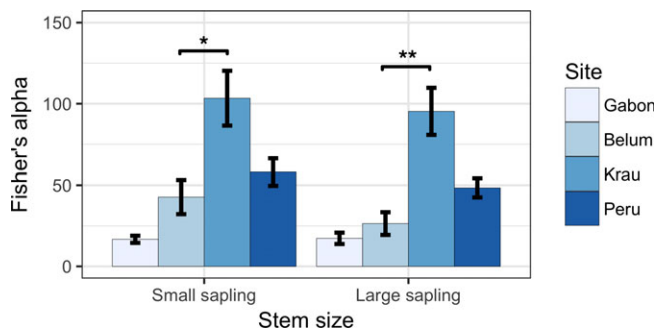


FIGURE 4. Diversity (Fisher's alpha) of small and large saplings in 100 m² strips in Belum and Krau, with comparative data from Gabon and Peru. Error bars indicate standard error. Asterisks and annotations indicate significance levels of statistical comparisons: * $P < 0.05$; ** $P < 0.01$.

(100.3 ± 42.6 [vs.] 42.7 ± 27.9 ; $t = -3.1$, $df = 10.1$, $P = 0.012$) and large (95.3 ± 38.5 [vs.] 26.4 ± 18.5 ; $t = -4.3$, $df = 8.6$, $P = 0.0023$) saplings (Fig. 4). Diversity in Peru (*ca* 60) was well below that at Krau but much higher than at Belum. Sapling diversity in areas of high elephant density in Gabon (10–15) was by far the lowest of any of the sites (Fig. 4).

DISCUSSION

Asian elephants, wherever they have been studied (China, India, Nepal, Sri Lanka, Myanmar, Malaysia), have been found to consume a mix of graze (grass and other monocots) and browse (McKay 1973, Sukumar & Ramesh 1995, Steinheim *et al.* 2005, Chen *et al.* 2006, Campos-Arceiz *et al.* 2008, Yamamoto-Ebina *et al.* 2016). Yet, to our knowledge, there have been no prior attempts to evaluate the impact of foraging by elephants on Asian rain forest dynamics. In the work reported here, we compared parameters of forest structure and biodiversity at two sites, Royal Belum State Park, in northern peninsular Malaysia where elephants are numerous, and the Krau Wildlife Reserve in central peninsular Malaysia where the last elephants were removed in 1993 and were rare for a long time before that.

Whereas there was no difference between the sites in the density of the smallest class of plants (<1 m tall), there were large differences in the densities of both small (≥ 1 m tall, <1 cm dbh) and large (≥ 1 cm dbh, <10 cm dbh) tree saplings, with higher densities occurring at Krau, where there are no elephants. There was also a striking difference between the two sites in the density of monocots, in that palms (*Calamus* spp. and others) were abundant at Krau but nearly absent from Belum. Notably, small (<1 m tall) non-palm monocots were abundant at Belum (*ca* 60/100 m²), but nearly absent from larger size classes.

The diversity of both small and large saplings, as represented by Fisher's alpha, was more than twice as great at Krau than at Belum. Sapling diversity in Peru fell between that at the two Malaysian sites and was higher at all three sites than in Gabon. Release from megafaunal herbivory could facilitate an increase in sapling diversity through higher survival of favored browse species. We noted a similar sharp increase in sapling diversity at an elephant-free site in Gabon (Terborgh *et al.* 2016b).

Break scars in saplings, a clear indicator of elephant foraging in Africa (Scheil & Salim 2004, Terborgh *et al.* 2016b), were equally prevalent at both Malaysian sites. This was an unexpected result that points to potential differences in the feeding behavior of African and Asian forest elephants and seems to negate a role of Asian elephants in tree dynamics, but raises the question of why breaks should be so much more frequent in Malaysia (72–76/100 stems) than in Peru (31/100 stems). Perhaps the background rate of stem breakage is higher in Malaysia, or alternatively, other megafauna present in Malaysia (tapirs, pigs) may be contributing to the frequency of breaks (see below). Breaks were strongly concentrated (58%) in the 0.1 m to 1.1 m height class at Belum, whereas 74% of the breaks at Krau were >1.1 m. Judging from Gabon, one would attribute the greater mean height of breaks at Krau to the work of elephants, but Krau was the elephant-free site. We have no explanation for this result other than the possibility of uncontrolled differences between the two Malaysian sites.

Pigs are one possible factor. Pigs can be abundant in Malaysian forests and are well-known to clip saplings to make nests (Ickes *et al.* 2003). We found an area of ~ 400 m² at Royal Belum where pigs had harvested saplings to make a nest. The saplings were small, mostly <1 cm dbh, and had been bitten off at a mean height around 0.4 ± 0.2 m. Most of the saplings (93.4% of 61 stems) had subsequently re-sprouted and appeared healthy. In addition, we were shown a number of saplings by our *orang asli* collaborators that had been bitten off by tapirs at heights around 0.8–1.0 m. Thus, large mammals are impacting tree regeneration in Malaysia by biting off saplings, even though our data are ambivalent with respect to the role of elephants in this process. We should also keep in mind that a few decades ago these forests would have contained rhinos and banteng as well as the surviving megafauna.

The question remains as to whether Asian elephants impact forest dynamics, and if so, how, or is it that pigs and tapirs are

the only surviving large mammals to do so? We found the densities of both small and large saplings to be low at Belum (vs.) Krau, and all monocots (except those <1 m tall) were scarce at Belum but abundant at Krau, especially palms. Asian elephants are known to consume large amounts of browse from a diversity of dicot species in forested environments (e.g., Sukumar & Ramesh 1995, Chen *et al.* 2006, Campos-Arceiz *et al.* 2008, Yamamoto-Ebina *et al.* 2016), but how do they do it in a way that leaves no evidence in the form of break scars? Many of the differences we found between Belum and Krau *could* be explained as consequences of elephant foraging if Asian elephants were to harvest saplings by pulling them up by the roots rather than breaking them mid-stem the way African forest elephants do. Harvesting whole saplings leaves no trace except depleted numbers of stems in the residual stand, something that is consistent with our findings at Belum.

A strong preference of Asian elephants for monocots is suggested by the fact that at Belum small monocots (<1 m) were well represented but larger ones, especially non-palm monocots, were almost absent (Fig. 2). In one set of observations, nearly 90% of the plants consumed by Asian elephants feeding in natural vegetation were monocots (Himmelsbach *et al.* 2006), an observation supported by Olivier (1978), who estimated a preference (measured as % in diet/% available) of 0.17 for dicot trees (vs.) 4.6 for palms in Peninsular Malaysia. Thus, the *prima facie* evidence suggests that Asian elephants exercise a strong preference for monocots but further investigation is needed before one can fully assess the role of elephants in the dynamics of closed-canopy evergreen forests in Asia.

ACKNOWLEDGMENTS

This study is part of the Management & Ecology of Malaysian Elephants (MEME), a joint research project between the Department of Wildlife and National Parks (DWNP) Peninsular Malaysia and the University of Nottingham Malaysia Campus (UNMC). Permits to conduct the research were kindly granted by DWNP (Krau Wildlife Reserve) and Perak's State Forest Corporation (Royal Belum State Park). Field activities were partially funded by grants from Mindset, UNMC's Interdisciplinary Centre for Environmental Studies (grant M0009.54.04) and Yayasan Sime Darby (grant M0005.54.04). Tok, Tok Sumpah, Param, Cherang, Param, Hussin, Khairil, and Ridzwan identified plants and led field activities; Alicia Solana-Mena, Angel Sanchez, Kim McConkey, Thomas Lai Yoke Hwa, and Arsir bin Abdul helped in the field; Ange Tan produced the map in Fig. S1; Praveena Chackrapani and Nurul Azuwa translated the abstract to the Malay language and helped with the logistics of the project. We are very grateful to all of them.

DATA AVAILABILITY

Data available from the Dryad Repository: <https://doi.org/10.5061/dryad.397vm> (Terborgh *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Map of Peninsular Malaysia and locations of Royal Belum State Park and the Krau Reserve. Blue dots in the map insets represent the location of the plots.

LITERATURE CITED

- ASNER, G. P., S. R. LEVICK, T. KENNEDY-BOWDOIN, D. E. KNAPP, R. EMERSON, J. JACOBSON, M. S. COLGAN, AND R. E. MARTIN. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. *Proc. Natl. Acad. Sci. USA* 106: 4947–4952.
- CAMPOS-ARCEIZ, A., T. Z. LIN, W. HTUN, S. TAKATSUKI, AND P. LEIMGRUBER. 2008. Working with mahouts to explore the diet of work elephants in Myanmar (Burma). *Ecol. Res.* 23: 1057–1064.
- CHEN, J., X. DENG, L. ZHANG, AND Z. BAI. 2006. Diet composition and foraging ecology of Asian elephants in Shangyong, Xishuangbanna, China. *Acta Ecol. Sin.* 26: 309–316.
- ENGLISH, M., G. GILLESPIE, M. ANCRENAZ, S. ISMAIL, B. GOOSSENS, S. NATHAN, AND W. LINKLATER. 2014. Plant selection and avoidance by the Bornean elephant (*Elephas maximus*) in the tropical forest: Does the plant recovery rate after herbivory influence food choices? *J. Trop. Ecol.* 30: 371–379.
- HIMMELSBACH, W., M. A. GONZALEZ-TAGLE, K. FULDNER, H. H. HOEFLE, AND W. HTUN. 2006. Food plants of captive elephants in the Okkan Reserved Forest, Myanmar (Burma), Southeast Asia. *Ecotropica* 12: 15–26.
- ICKES, K., S. J. DEWALT, AND S. C. THOMAS. 2003. Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. *J. Ecol.* 91: 222–233.
- KERLEY, G. I. H., AND M. LANDMAN. 2006. The impacts of elephants on biodiversity in the Eastern Cape subtropical thickets. *S. Afr. J. Sci.* 102: 395–402.
- McKAY, G. M. 1973. The ecology and behavior of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contribut. Zool.* 125: 1–113.
- MERWE, N. J., J. A. THORP, AND R. H. BELL. 1988. Carbon isotopes and indicators of elephant diets and African environments. *Afr. J. Ecol.* 26: 163–172.
- OKSANEN, J., BLANCHET, F. G., KINDT, R., LEGENDRE, P., MINCHIN, P. R., O'HARA, R. B., SIMPSON, G. L., SOLYMOS, P., STEVENS, M. H. H., AND WAGNER, H. 2015. *vegan: Community Ecology Package*. R package version 2.3-2.
- OLIVIER, R. C. D. 1978. On the ecology of the Asian elephant. PhD dissertation. University of Cambridge, UK.
- OWEN-SMITH, R. N. 1988. *Megaherbivores: The influence of very large body size on ecology*. Cambridge University Press, Cambridge, UK.
- R Core Team. (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- RUTINA, L. P., S. R. MOE, AND J. E. SWENSON. 2005. Elephant *Loxodonta Africana* driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*. *Wildl. Biol.* 11: 207–213.
- SCHEIL, D., AND A. SALIM. 2004. Forest tree persistence, elephants, and stem scars. *Biotropica* 36: 506–521.
- SHORT, J. 1981. Diet and feeding behavior of the forest elephant. *Mammalia* 45: 177–185.
- SKARPE, C., P. A. AARRESTAD, H. P. ANDREASSEN, S. S. DHILLON, T. DIMAKATSO, J. T. du TOIT, D. J. HALLEY, H. HYTTBORN, S. MAKHABU, M. MARI, AND W. MAROKANE. 2004. The return of the giants: Ecological effects of an increasing elephant population. *Ambio* 33: 276–282.

- STEINHEIM, G., P. WEGGE, J. I. FJELLSTAD, S. R. JNAWALI, AND R. B. WELADJI. 2005. Dry season diets and habitat use of sympatric Asian elephants (*Elephas maximus*) and greater one-horned rhinoceros (*Rhinoceros unicornis*) in Nepal. *J. Zool.* 265: 377–385.
- STRUHSAKER, T. T., J. S. LWANGA, AND J. M. KASENENE. 1996. Elephants, selective logging and forest regeneration in the Kibale Forest, Uganda. *J. Trop. Ecol.* 12: 45–64.
- SUKUMAR, R. 2003. The living elephants: Evolutionary ecology, behavior, and conservation, p. 483. Oxford University Press, New York, NY.
- SUKUMAR, R., AND R. RAMESH. 1995. Elephant foraging: Is browse or grass more important? *In* J. C. Daniel, and H. Datye (Eds.). *A week with elephants*, pp. 368–374. Bombay Natural History Society, Bombay and Oxford University Press, New Delhi.
- TERBORGH, J., L. C. DAVENPORT, R. NIANGADOUMA, E. DIMOTO, J. C. MOUANDZA, O. SCHULTZ, AND M. R. JAEN. 2016a. The African rainforest: Odd man out or megafaunal landscape? African and Amazonian forests compared. *Ecography* 38: 187–193.
- TERBORGH, J., L. C. DAVENPORT, R. NIANGADOUMA, E. DIMOTO, J. C. MOUANDZA, O. SCHULTZ, AND M. R. JAEN. 2016b. Megafaunal influences on tree recruitment in African equatorial forests. *Ecography* 38: 180–186.
- TERBORGH, J., L. C. DAVENPORT, L. ONG, AND A. CAMPOS-ARCEIZ. 2017. Data from: Foraging impacts of Asian megafauna on tropical rain forest structure and biodiversity. Dryad Digital Repository. <https://doi.org/10.5061/dryad.397vm>.
- TIESZEN, L. L., T. W. BOUTTON, W. K. OTTICHILO, D. E. NELSON, AND D. H. BRANDT. 1989. An assessment of long-term food habits of Tsavo elephants based on stable carbon and nitrogen isotope ratios of bone collagen. *Afr. J. Ecol.* 27: 219–226.
- WHITE, L. J. T., C. E. G. TUTIN, AND M. FERNANDEZ. 1993. Group composition and diet of forest elephants, *Loxodonta africana cyclotis*, Matchie 1900, in the Lopé Reserve, Gabon. *Afr. J. Ecol.* 31: 181–199.
- WOODRUFF, D. S. 2003. The location of the Indochinese-Sundaic biogeographic transitions in plants and birds. *Nat. Hist. Bull. Siam. Soc.* 41: 97–108.
- YAMAMOTO-EBINA, S., S. SAABAN, A. CAMPOS-ARCEIZ, AND S. TAKATSUKI. 2016. Food habits of Asian elephants *Elephas maximus* in a rainforest of northern Peninsula Malaysia. *Mammal Study* 41: 151–161.