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Authors: Lindsell, Jeremy A. , Lee, David C. , Powell, Victoria J. , and Gemita, Elva

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Research Article

Availability of large seed-dispersers for restoration of degraded tropical forest

Jeremy A. Lindsell[1,4]*, David C. Lee[2,3], Victoria J. Powell[2], and Elva Gemita[2]

[1] RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire SG19 2DL, UK

[2] Harapan Rainforest, Jalan Dadali 32, Bogor 16161, West Java, INDONESIA

[3] School of Applied Sciences, The University of South Wales, Pontypridd CF37 4AT, UK

[4] A Rocha International, 3 Hooper Street, Cambridge CB1 2NZ UK

* Corresponding author: Jeremy Lindsell (jeremy.lindsell@gmail.com)

Abstract

An estimated 63% of Southeast Asian forests are classed as disturbed and secondary as a result of human activity. Many of these forests remain important for biodiversity conservation and ecosystem services so there is much interest in their capacity for restoration. The role of larger animals as seed dispersers in natural regeneration is well-attested since they are often the only agent by which large-seeded trees can effectively disperse. This is especially important for late successional shade-tolerant species which might otherwise be excluded from disturbed sites. However, many larger animals are sensitive to habitat degradation so may be lost from the very areas that require them. We investigated the persistence of a suite of large mammals that are known seed-dispersers and are also threatened species, in a degraded site in lowland south-central Sumatra. We used camera traps and field observations to relate their distributions to prevailing vegetation conditions. Although most species were more frequently detected in the more intact areas, most were able to occupy habitats with high levels of disturbance and population densities were relatively high. It is clear that severe habitat degradation does not necessarily lead to the immediate loss of large-bodied seed dispersers, so ensuring adequate protection for these species from external threats, such as hunting, must be built into management plans for restoration concessions.

Key words: seed dispersal; restoration; Southeast Asia; degraded forest; camera-trap

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Introduction

The extent and condition of forest cover in Southeast Asia is diminishing at a rapid rate [1]. Whether this trend is biologically reversible will depend on the availability and propensity of cleared and degraded forest land for regrowth and restoration [2]. The area of degraded forest is large though the degree of degradation varies greatly [3]. Prospects for restoring degraded forests will depend, in part, on the resilience of key ecological processes [4-5]. In particular, forest regeneration will depend on the availability of animals to act as seed dispersers. The role of larger animals in seed dispersal is especially important since they are often the only agent by which large-seeded trees can effectively disperse [6-7], and they also tend to undertake longer distance movements [8]. This is especially important for late successional shade-tolerant trees which might otherwise be excluded from recolonising disturbed sites in the absence of seed dispersers [9]. However, forest degradation has serious consequences for forest biodiversity and many larger animals may be lost from the very areas that depend on their dispersal services. Nonetheless, although it may be argued that degraded forest is no substitute for pristine forest [10], degraded forests can retain a significant proportion of their original fauna [11-12].

Besides habitat degradation, many tropical forests are also subject to intense and increasing hunting pressure especially as demand for bushmeat and animal parts increases [13-15]. In the absence of habitat degradation, hunting pressure alone is capable of defaunating a forest [16]. The impacts of defaunation on forest dynamics are increasingly recognised including changes to tree recruitment [17], tree dispersal [18] and a wide range of other ecological and evolutionary processes [19].

Within Indonesia as much as 20% of the entire forest estate (some 25 million hectares) is currently classified as unlicensed production forest [20], most of which comprises exhausted logging concessions. Whether or not these kinds of degraded sites can be restored through the promotion of natural processes could have significant implications for their future management, so a critical question is the extent to which natural seed dispersal can be expected to operate. We investigated this question in an Ecosystem Restoration concession in south central Sumatra. Harapan Rainforest was the first Ecosystem Restoration concession established in Indonesia and comprises c. 98,000 ha of heavily logged and cleared lowland forest. Our aim was to investigate whether such exhausted production concessions can still support significant levels of their original animal diversity at population densities that might ensure natural seed dispersal processes can operate effectively. In particular we asked:

1. Which potential seed dispersers are resilient to degradation as evidenced by their persistence in Harapan Rainforest?
2. At what levels of richness and abundance do seed dispersers occur at across the site?
3. How should we judge conditions in this degraded site in the light of findings elsewhere in the region?

Methods

Harapan Rainforest lies in the eastern lowlands of Sumatra (103°17'49¨E, -2°12'94¨S) on dryland soils with an elevation ranging from 30-120 m asl. The site covers 985.5 km^2 of previously logged forest, most of it heavily logged, and in some places at least twice (Fig. 1). Some areas have been cleared and burned for agriculture. The site is surrounded by industrial oil palm, rubber and acacia plantations and small-scale agriculture. In the least disturbed areas the forest has a mixed species composition typical of lowland rain forest. More degraded areas have an open canopy dominated by *Macaranga* species and a non-native pioneer tree *Bellucia pentamera*, but lacks large trees and often has a dense understorey of herbs (typically Zingerberaceae and Marantaceae) [21-23].

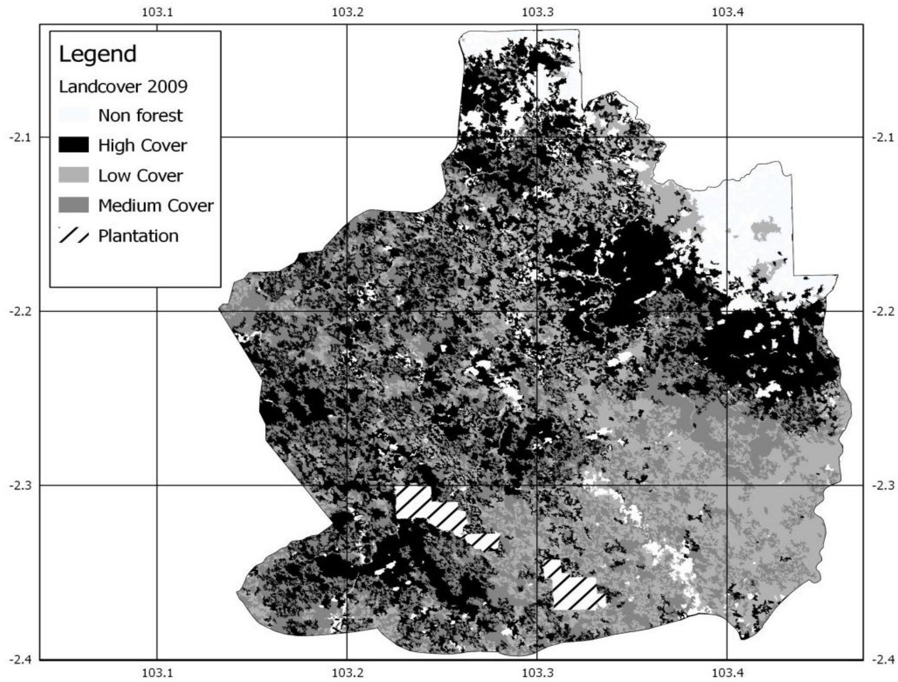

Fig. 1. Landcover map of Harapan Rainforest, Sumatra, in 2009 showing the complex nature of the remaining forest cover. Plantations shown are of overgrown *Acacia mangium* and non-forest areas comprise scrub, open fields and burned areas. Adapted from Schweter (2009).

Terrestrial mammals were surveyed using digital camera traps (Reconyx Inc.) deployed on a regular grid across the site [22]. Camera placement was unbiased by animal sign and deployment period was typically 30 days. We calculated encounter rates for each species from each camera location based on the number of independent photographs of a species. Independence was defined by a lapse of at least 60 minutes between successive photographs. The inverse of the encounter rate – number of days to acquire a photograph – was used to compare the study site with equivalent figures published for particular species from other sites in the region. There has been some criticism of the use of uncorrected encounter rates as indices of relative abundance [24]. However studies of both carnivores [25] and ungulates [26] have found a linear relationship between camera trapping rate and density measured by alternative methods and the metric has been widely used [27-31]. Here we draw no conclusions about the precise relationship between encounter rate and density or abundance. We report (naïve) levels of occupancy and compare these with the trapping rate to test whether more widely occurring species were also encountered more frequently.

Seed dispersing larger terrestrial mammals were ranked according to Corlett [6], with some modification in light of subsequent data [32]. The ranking accounted for the capacity and propensity of the species to ingest or carry seeds rather than chew or immediately discard them, typical movement distances of the animals, the range of tree species they might consume, and where available a more detailed understanding of the viability of excreted seed.

Forest habitat at camera locations was scored as having high or low levels of canopy cover according to a ground-truthed classification of a SPOT satellite image acquired concurrently with the data collection [21].

Results

Camera trapping data were collected at 148 locations across the site over 4155 trapping days. Table 1 lists the proportion of occupied locations and encounter rates of the key species and groups recorded. Many dispersers were recorded at a high number of individual camera locations. The most prevalent species were the macaques, pigs and deer, but even civets (all species pooled), Sun Bears (*Helarctos malayanus*) and Malayan Tapirs (*Tapirus indicus*) were recorded at around a third of locations. There were only 10 locations (7%) that lacked any records at all of potential dispersers. When the data were supplemented by species lists from other research at HRF [22], most species and groups of dispersing mammals considered by Corlett [6] were present at the site, the key exceptions being Orang-utan (*Pongo abelii*) and Sumatran Rhinoceros (*Dicerorhinus sumatrensis*).

Table 1. Naïve occupancy rates (percentage of camera locations with species recorded present) and number of independent photos for each of the larger mammalian seed dispersers recorded in Harapan Rainforest, Sumatra.

Species	% occupancy	Photos
Pig-tailed Macaque *Macaca nemestrina*	83.1	725
Red Muntjac *Muntiacus muntjak*	59.5	324
Eurasian Wild Pig *Sus scrofa*	57.4	424
Lesser Mouse Deer *Tragulus kanchil*	45.3	191
All civets	*33.1*	*100*
Malayan Tapir *Tapirus indicus*	29.7	85
Sun Bear *Helarctos malayanus*	28.4	70
Bearded Pig *Sus barbatus*	25.0	301
Malay Civet *Viverra tangalunga*	18.9	46
Sambar *Rusa unicolor*	14.9	30
Common Palm Civet *Paradoxurus hermaphroditus*	10.8	32
Greater Mouse Deer *Tragulus napu*	6.1	24
Banded Palm Civet *Hemigalus derbyanus*	4.1	9
Masked Palm Civet *Paguma larvata*	2.7	8
Binturong *Arctictis binturong*	2.7	4
Small-toothed Palm Civet *Arctogalidia trivirgata*	0.7	1

The mean encounter rate for each species was highly correlated with the proportion of locations occupied (r^2=0.94, p<0.001; Fig. 2). A notable outlier in this relationship was Bearded Pig (*Sus barbatus*) which was recorded at far fewer locations relative to its encounter rate compared with other species. When the mean encounter rate was adjusted by removing the effect of unoccupied sites, the relationship weakened considerably though remained significant (r^2=0.44, p<0.002).

The species richness of dispersers was relatively uniform across the site with many locations recording multiple species (Fig. 3A). By contrast the encounter rates recorded at camera locations varied more strongly across the site (Fig. 3B) indicating higher levels of disperser activity in some locations. Nonetheless, log richness (adjusted for effort) and log encounter rate were highly correlated at camera locations (r^2=0.69, p<0.001).

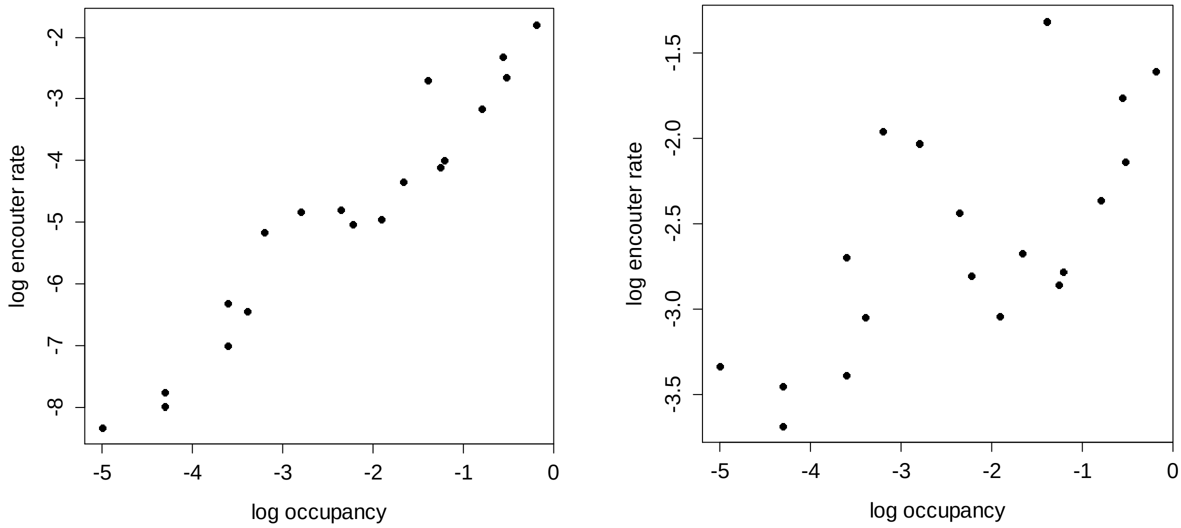

Fig. 2. The increase in log encounter rate (n per day) with log occupancy of mammalian seed dispersers in Harapan Rainforest, Sumatra. Each point represents an individual species. A single location with a very high encounter rate of *Sus barbatus* has been excluded, as have all locations with fewer than 15 days of data. a) unoccupied locations included in calculation of mean encounter rates; b) unoccupied locations excluded from calculation of mean encounter rates.

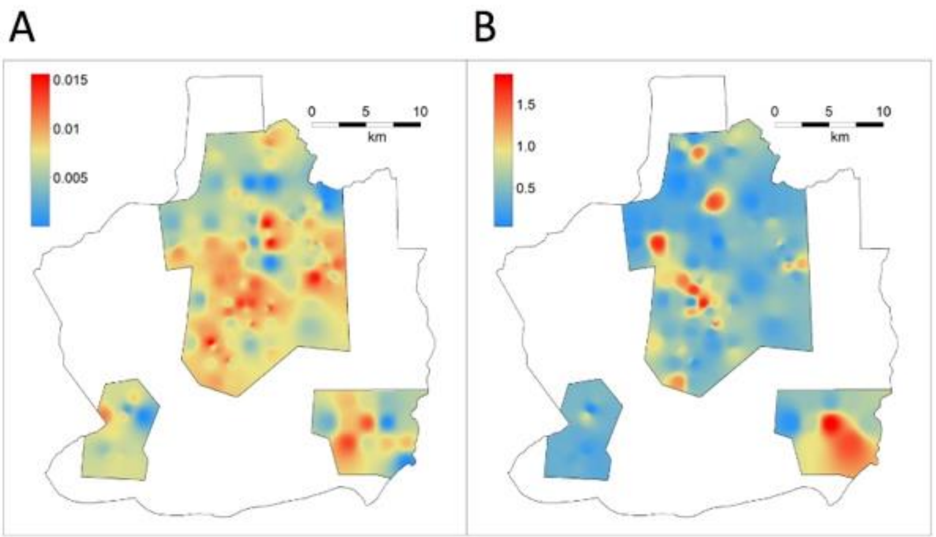

Fig. 3. (A) Interpolated estimates of variation in mammalian disperser species richness adjusted by camera deployment period and, (B) mammalian disperser encounter rates (n per day; all species pooled) in Harapan Rainforest, Sumatra. Interpolation between camera locations was by inverse distance weighted averaging.

When the encounter rates were disaggregated into individual species, species such as Pig-tailed Macaque (*Macaca nemestrina*), which are rather generalist in their requirements, were found to be widespread across the site, whereas more forest dependent species such as Sun Bear and Malayan Tapir appear to be concentrated in the centre of the site (Fig. 4).

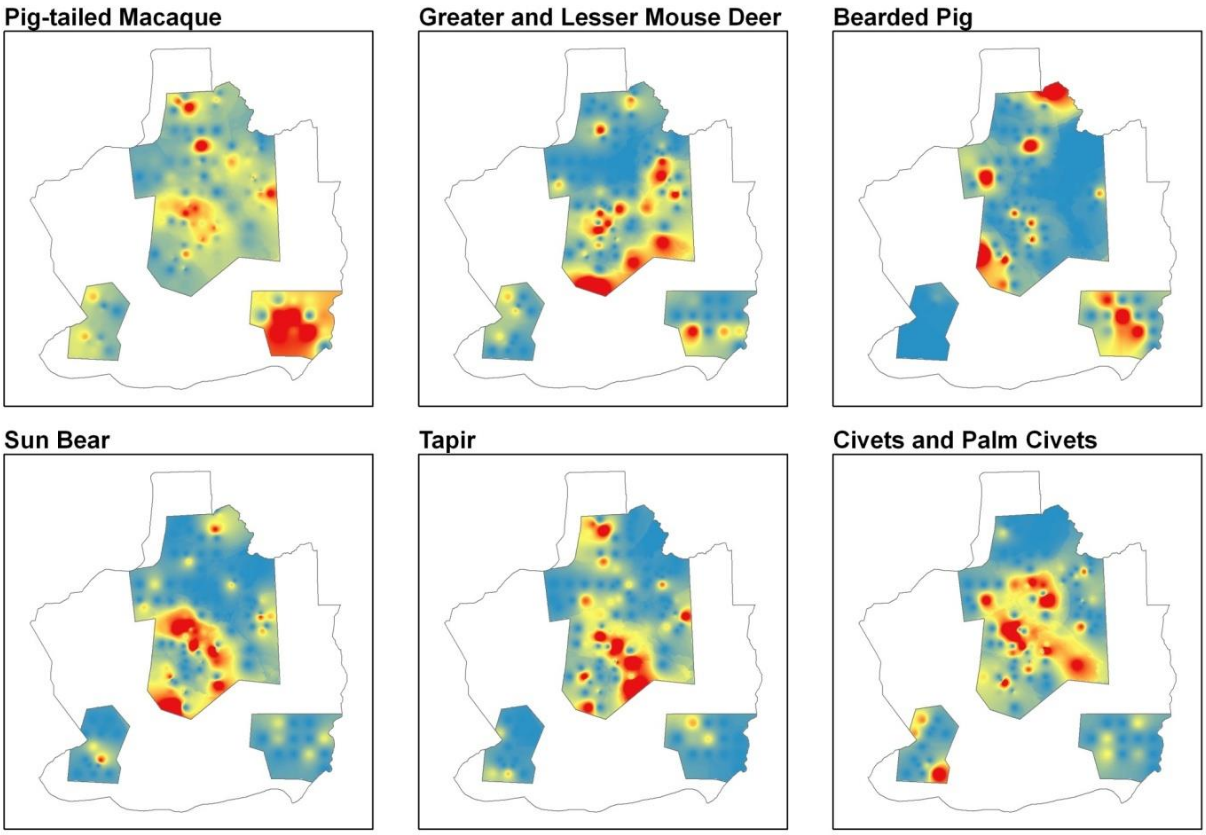

Fig. 4. Interpolated estimates of variation in mammalian disperser encounter rates (n per day) in Harapan Rainforest, Sumatra. Interpolation between camera locations was by inverse distance weighted averaging.

Comparison of encounter rates by forest type with species ranked by disperser quality showed some evidence that poorer dispersers tended to be found in the more degraded habitat, but there was little evidence that the better dispersers were less prevalent in the poorer habitats (Fig. 5).

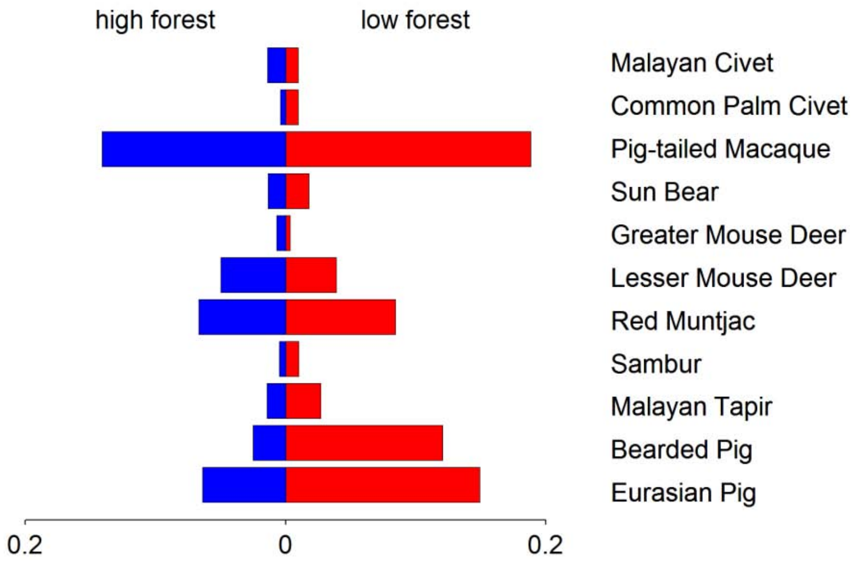

Fig. 5. Variation in mammalian disperser encounter rates (n per day) according to forest condition in Harapan Rainforest, Sumatra. Species are arranged top to bottom in order of decreasing disperser value following Corlett [6].

For a range of species recorded at the cameras, encounter rates were compared with published figures from elsewhere in the region. For most of the species we considered, the mean encounter rate was far higher in our study site than in a number of well-established protected areas in the region (Table 2).

Table 2. Comparison of camera trapping rates for large mammals in forests of Southeast Asia. The number shown is the mean number of days between successive photos. ' - ' indicates that no data were available.

Species	HRF	BBS	KS	TN	Ranking
Pig-tailed Macaque	6	13	-	351	**HRF** > BBS > TN
Sun Bear	57	-	47	62	KS > **HRF** > TN
Mouse Deer	19	86	-	107	**HRF** > BBS > TN
Red Muntjac	12	41	-	25	**HRF** > BBS > TN
Sambar	128	182	-	44	TN > **HRF** > BBS
Malayan Tapir	48	80	61	26	TN > **HRF** > KS > BBS
Eurasian Pig	9	28	-	28	**HRF** > BBS/TN

HRF: Harapan Rainforest. BBS: Bukit Barisan Selatan, Sumatra [28]; KS: Kerinci Seblat, Sumatra [27, 29]; TN: Taman Negara, Peninsular Malaysia [33].

Discussion

The most striking result from our survey of terrestrial mammalian seed dispersers in a degraded lowland forest in Sumatra is that a high diversity of species were retained and at comparatively high levels of occupancy, despite high levels of habitat degradation. These species can therefore be regarded as resilient to degradation, at least in the timescale we measured. Across the site, a diversity of dispersers was available with a range of body sizes, suggesting that functional diversity as well as species diversity were ubiquitous. Although encounter rates varied across the site, there were few areas that lacked records of dispersers altogether in the duration of our sampling. If the camera data have provided a fair indication of the diversity and levels of activity by mammalian seed dispersers then these results suggest that even within the most degraded areas of forest, where inward movement of tree seeds and regeneration is most needed, these processes are likely to be prevalent.

A number of explanations of the observed high diversity and apparent abundance of terrestrial mammals present themselves. Firstly, it is important to note that the site is entirely lowland whereas the comparison sites often included substantial areas at higher altitude. Animal densities may normally be higher at lower altitudes, though it is noted that this is not always the case [34]. Secondly, immigration from surrounding areas may have led to an artificial inflation of densities within the study site. As noted, much of the surrounding landscape has been converted to oil palm, rubber and acacia plantations, such that there is little natural or semi-natural habitat remaining outside the study site. It is possible that larger animals relocated in order to avoid disturbance in these surrounding areas. This explanation seems fairly unlikely as we would expect density dependent effects to have already compensated for such inward movements, but it cannot be entirely ruled out. It is also possible that some species – such as the pigs – are benefiting from changes in the surrounding landscape as has been noted in peninsular Malaysia [35]. Thirdly, since past logging was most heavily concentrated on dipterocarp species it is possible their removal had limited impact on frugivore food supply since dipterocarps tend to form a relatively low proportion of frugivore diets. Indeed removal of dipterocarps may even have given fleshy fruit bearing tree species a competitive advantage. The fourth possibility is that the prevalence of an invasive alien tree *Bellucia pentamera* in the site has in some way compensated for the levels of disturbance. This is entirely a hypothesis but has some merit since it is clear that this heavily-fruiting pioneer species is widespread throughout the concession. At present, the significance of this tree in the diet of the species under consideration is unknown though initial observations suggest that it may not be selected by frugivorous birds (I. Fitriawan pers. comm., 2013). Finally, it seems fairly certain that the status of wildlife in the area is in part attributable to low hunting levels. Although we lack formal data on hunting activity in the site, there is no evidence that hunting pressure is anything other than low (pers. obs.), which is in contrast to reports from other protected areas in the region.

Our observations of terrestrial mammals surveyed using camera traps accord well with the results of conventional surveys of Agile Gibbons (*Hylobates agilis*) in the same site. These too have been found to occur at high densities, including within the more degraded parts of the forest [36]. For the gibbons too it is possible that their numbers were boosted by the prevalence of *B. pentamera* though again we currently lack firm evidence that this tree forms a significant part of their diet.

It should be noted however that it is not inevitable that the presence of dispersers is actually resulting in dispersal, or dispersal of the right kind. Where fruit crops have a patchy distribution due to habitat degradation it is possible that some dispersers reduce their movements in order to remain close to the available food sources and thus reduce the distance that seeds may be moved. The assumption that a range of dispersers of a range of sizes must imply that a range of trees can be effectively dispersed may also be invalid if habitat degradation leads to a reduction in fruit diversity and simplification of the food sources.

It is also important to note that a number of dispersing species can also be seed predators [37] as well as herbivores, and their net impact on a degraded and regenerating forest is unclear. The pig species, for example, are known to have a considerable impact on the forest understory [38-40] and Lesser Mouse Deer (*Tragulus kanchil*) can be graminivorous [40]. We did not consider here other, smaller, species that are more typically seed predators (e.g. Malayan Porcupine *Hystrix brachyura*) and which may also have responded to habitat degradation with changes in abundance.

Despite these provisos, our observations show no evidence that Harapan Rainforest is significantly defaunated as a result of habitat degradation or hunting. As such, the site is likely to benefit from all the dispersal services that the observed range of animals can provide. All of these species (or analogous species) are ubiquitous in the Southeast Asian forests where they have not been extirpated by hunting. Our observations from Harapan Rainforest demonstrate that these species can be resilient to significant habitat degradation and are therefore able to comprise an important part of the process of restoring forests in the region. This therefore highlights the importance of ensuring adequate protection of these species within commercial concessions that are earmarked for restoration.

Implications for conservation

Ecosystem restoration concessions provide good prospects for biodiversity conservation outside the protected area network in areas that have already experienced significant vegetation degradation. We have shown that providing hunting pressure is low, such areas can harbour significant populations of many large mammals including some globally threatened species. Many of these species are important tree seed dispersers so can be expected to play an important role in the recovery of the vegetation in these areas, thus directly fulfilling the aims of such concessions. The effective protection of large mammals in these concessions is therefore a win-win scenario for both forest restoration and biodiversity conservation. The biodiversity value of these sites needs to be recognized and to constitute a central consideration in their management plans, with obligations placed on concession holders to provide effective protection for wildlife within their concession.

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