

# Selective logging causes the decline of large-sized mammals including those in unlogged patches surrounded by logged and agricultural areas

Jamaluddin Jamhuri<sup>a</sup>, Liza D. Samantha<sup>a</sup>, Sze Ling Tee<sup>a</sup>, Norizah Kamarudin<sup>a</sup>,  
Adham Ashton-Butt<sup>b</sup>, Akbar Zubaid<sup>c</sup>, Alex M. Lechner<sup>d</sup>, Badrul Azhar<sup>a,e,\*</sup>

<sup>a</sup> Faculty of Forestry, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia

<sup>b</sup> School of Biological Sciences, University of Southampton, Southampton SO17 1BJ, United Kingdom

<sup>c</sup> Faculty of Science and Technology, National University of Malaysia, 43600 Bangi, Selangor, Malaysia

<sup>d</sup> School of Environmental and Geographical Sciences, University of Nottingham Malaysia Campus, 43500 Semenyih, Selangor, Malaysia

<sup>e</sup> Biodiversity Unit, Institute of Bioscience, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia

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## ABSTRACT

Legal and illegal logging is prevalent throughout the tropics, impacting on natural habitat and wildlife. This study aimed to investigate the sensitivity of forest mammals to selective logging in the lowland dipterocarp forests of South-West Peninsular Malaysia and identify the underlying factors that determine species occurrence. A total of 120 camera trap locations were deployed within selectively logged and unlogged forests. We found that unlogged forest had greater wildlife occurrences compared to selectively logged forests, including two endangered mammal species not found in logged forest. Forest vegetation structure characteristics such as the abundance of lianas, large trees, saplings, palms, bamboo and seedlings were associated with mammal species richness. Mammal species richness increased with number of forest trees, particularly those with a DBH of > 45 cm, but this was limited to high altitude forest. Worryingly, we did not detect any large mammalian apex predators such as leopards or tigers in either unlogged or selectively logged forests. The absence of these animals may be the result of poaching, habitat degradation or other pressures; these mammals are expected to be present in intact forests in Peninsular Malaysia. Restoring logged forests and preserving the remaining unlogged lowland dipterocarp forests are critically important to safeguard mammalian biodiversity in the region. Besides that, we recommend that conventional logging practices are replaced with reduced impact logging methods.

## 1. Introduction

Tropical forests globally are being threatened by logging, fragmentation, and degradation (Edwards et al., 2014; Gaveau et al., 2014; Abood et al., 2015; Barlow et al., 2016). The increase in forest loss and degradation has significant repercussions for climate change mitigation and biodiversity conservation (Margono et al., 2014). Two hundred and forty million hectares of natural forest has been cleared worldwide from 1990 to 2015 for purposes of agricultural expansion and urban development (FAO, 2016). Tropical forest area declined at a rate of 5.5 M ha y<sup>-1</sup> between 2010 and 2015 (Keenan et al., 2015).

Such drastic changes in forest cover will impact on forest ecosystems and wildlife. Forest conversion to oil palm plantations, a major driver of forest loss in Southeast Asia, has caused significant changes to species compositions and abundances due to the sensitivity of wildlife to landscape modification (Bernard et al., 2014; Fitzherbert et al.,

2008). Logging is another major driver of forest loss and degradation in Southeast Asia; in Malaysian Borneo species richness in newly logged areas declined by 11%, but areas that were logged more than a decade ago had the same levels of species richness as in old-growth forest (Brodie et al., 2015). However, for some species such as primate and ungulate species, anthropogenic threats from hunting posed greater risks than logging and were particularly severe for biologically significant fauna such as seed dispersers and herbivores (Brodie et al., 2015).

High demand for timber products has led to high rates of harvesting in Southeast Asia that has consequently contributed to a loss of biodiversity (Sodhi et al., 2004; Yamada et al., 2014). Commercial logging in Southeast Asia, commonly based on selective logging techniques, mainly targets dipterocarp species when the trees reach a particular height. Thus vertebrates relying on these trees are adversely affected (Johns, 1985; Meijaard et al., 2005). However, recent studies have

\* Corresponding author at: Faculty of Forestry, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia.

E-mail address: [b.azhar@upm.edu.my](mailto:b.azhar@upm.edu.my) (B. Azhar).

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shown that even after logging these forests are still of high conservation value for wildlife, though many species are negatively impacted (Edwards et al., 2011; Gibson et al., 2011; Putz et al., 2012). Selective logging appears to be the potential cause of species extinction of animals in Southeast Asia such as Malayan tiger *Panthera tigris*, Asian sunbear *Helarctos malayanus* and Asian tapir *Tapirus indicus* (Pimm and Raven, 2000; Okuda et al., 2003; Bischoff et al., 2005).

Tropical forest degradation from selective logging can also cause significant changes to species composition and abundances through the creation of secondary forests or logged forests (McMorrow and Talip, 2001). Secondary forest consists of naturally regenerating forest that has experienced a significant loss of the original vegetation, either at a single point in time or over a prolonged period. Secondary forest often differs greatly in forest structure and tree composition compared to comparable primary forests sites (FAO, 2003). Selective logging can modify interactions between species and ecological processes causing a decline in wildlife populations, imbalances in ecosystems and extinction of native species (Cowlishaw et al., 2009; Sasaki and Putz, 2009; Mayor et al., 2015; Magrach et al., 2016; Olsoy et al., 2016). Species richness of invertebrates, amphibians, and mammals decline as logging intensifies, but these effects vary with taxonomic group and continental location (Burivalova et al., 2014). However, selectively logged forests are quite similar to primary forests in terms of the possibility for thermal buffering and ensuing capability to preserve temperature-sensitive species under climate change (Senior et al., 2018).

In Malaysia, where our study takes place, a Reduced Impact Logging (RIL) system has been implemented to reduce the ecological impacts from forestry (Tay, 1999; Bicknell et al., 2014; Nagulendran et al., 2016). In areas where RIL has been used biodiversity effects are noticeably less intense, unlike where conventional methods are applied (Azevedo-Ramos et al., 2006; Bicknell et al., 2014). RIL includes skid trail planning and directional felling techniques to avoid soil damage that can reduce plantation or pasture productivity for decades (Putz et al., 2008) and can reduce adverse impacts on ecosystem functions and services (Edwards et al., 2011; Putz et al., 2012). However, recent studies suggest that the effects of RIL are minimal on non-volant mammals and birds (Azevedo-Ramos et al., 2006; Wunderle et al., 2006) and negligible on other species, but may increase biodiversity for some taxa via the increase in habitat heterogeneity (Castro-Arellano et al., 2007). Nevertheless, Burivalova et al. (2015) suggest that the influences of logging can be lessened through forest management approaches such as increasing the rotation cycle and executing RIL.

The response of forest mammals to selective logging are poorly understood due to their cryptic behaviour and low densities. Hence, this study aimed to understand the long-term effects to forest mammals of selective logging. We did this by quantifying differences in species richness and composition between forty-year old logged forest and unlogged forest. In addition, we assessed key habitat quality characteristics which drive those differences. Our data will provide vital information for forest managers for better post-logging forest wildlife management and conservation in the tropics.

## 2. Methods

### 2.1. Study area

Our study area was located in a contiguous forested landscape in the southwest of Peninsular Malaysia, comprising the states of Selangor and Negeri Sembilan (Fig. 1). The study areas were classified into two types: unlogged forest (latitude 2°33'58.95"N and longitude 102°11'56.76"E) and selectively logged forest (latitude 6°6.07"N and longitude 101°52'50.29"E) with an average altitude of 163 to 505 m. The study areas are characterized by lowland dipterocarp forest. Both logged and unlogged forests were physically connected despite these forests being located in different states. Logged areas and oil palm plantations surround the unlogged forest. Timber extraction occurred 40 years ago in

the logged forest. The logging in the study areas followed the Selective Management System, developed in the late 1970s (Meijaard et al., 2005). This system allows the extraction of all commercial species with a DBH > 45 cm for non-dipterocarps, and > 50 cm for dipterocarps. The Selective Management System aims to maintain sufficient regeneration potential in the logged forest areas to allow re-harvesting thirty years later, with a minimum of 32 stems of commercial species in the 30–45 cm DBH size class maintained per hectare (Hadi et al., 1987; Appanah, 1998).

### 2.2. Animal sampling

A systematic sampling design was used. We selected a starting point at least 500 m from forest edge at random and then systematically located succeeding points at set distances (minimum of 500 m apart) from this (Morrison et al., 2008). Camera traps (Bushnell 8MP Trophy Cam HDs with Night Vision) were deployed at 120 locations in the logged and unlogged forests (60 cameras in each forest type) (Fig. 1). The cameras were installed in the forests based on the following considerations and as close to pre-selected points as possible: availability of access routes; presence of visible animal trails; and tree marks by wildlife; footprints and scars (Bernard et al., 2014; Sasidhran et al., 2016).

Each camera was geo-referenced using a Global Positioning System (GPS) (Garmin 78) with a minimum accuracy of 5 m. Cameras were left in the forests for a month without using bait. Nichols and Karanth (2002) recommended that two weeks is the minimum sampling period, but we doubled the time from two weeks to four weeks in order to increase the probability of detecting wildlife present in both study areas. Due to limited number of camera traps, only 25 camera traps were used simultaneously in unlogged and logged forests. We conducted the camera trapping survey in three trapping periods from May 2015 until April 2016. We identified the survey months as either dry (January – February and May – September) or wet (March – April and October – December) and included season in the analysis.

All camera traps were attached to the base of trees approximately 0.5 m above the ground, with the camera lenses facing outwards. When triggered, the camera traps were set to take three images with a one-second interval between them. The passive infrared motion sensor was set to a normal setting, so that it could detect any movement that passed in front of the camera (Bernard et al., 2014; Mohd-Azlan and Sharma, 2003; Sasidhran et al., 2016). The camera comes with a night-vision feature that enables it to function day and night. This method of setting up the camera traps has proved to be effective in studying the occurrence of elusive mammal species in tropical forest in previous studies (Kawanishi and Sunquist, 2004; Azlan et al., 2006; Bernard et al., 2014; Sasidhran et al., 2016).

### 2.3. Assessment of habitat quality characteristics

We measured ten characteristics of stand-level habitat quality at each camera trap location in the unlogged and logged forests (Table 1). A plot size of 50 m × 20 m (0.01 ha) was established. Characteristics included: i) number of trees with diameter above 45 cm at breast height (DBH), ii) number of trees with DBH below 45 cm, iii) number of bamboo clumps, iv) number of liana species, v) number of palm trees, vi) number of fallen trees, vii) number of saplings (1–5 cm DBH), viii) number of seedlings i.e. woody plants smaller than 1 cm DBH, ix) percentage of light gaps, and x) altitude.

The number of saplings was recorded within a 5 m × 5 m plot, while the number of seedlings was recorded within a 2 m × 2 m plot, both within the 50 m × 20 m plot area. Percentage of light gaps was measured using a digital camera in a near-vertical and skyward direction, at 4 points taken randomly within the 50 m × 20 m plot area. The images captured by the camera were then analysed using MATLAB 7.1 to estimate canopy cover, with a light gap image analysis script created by

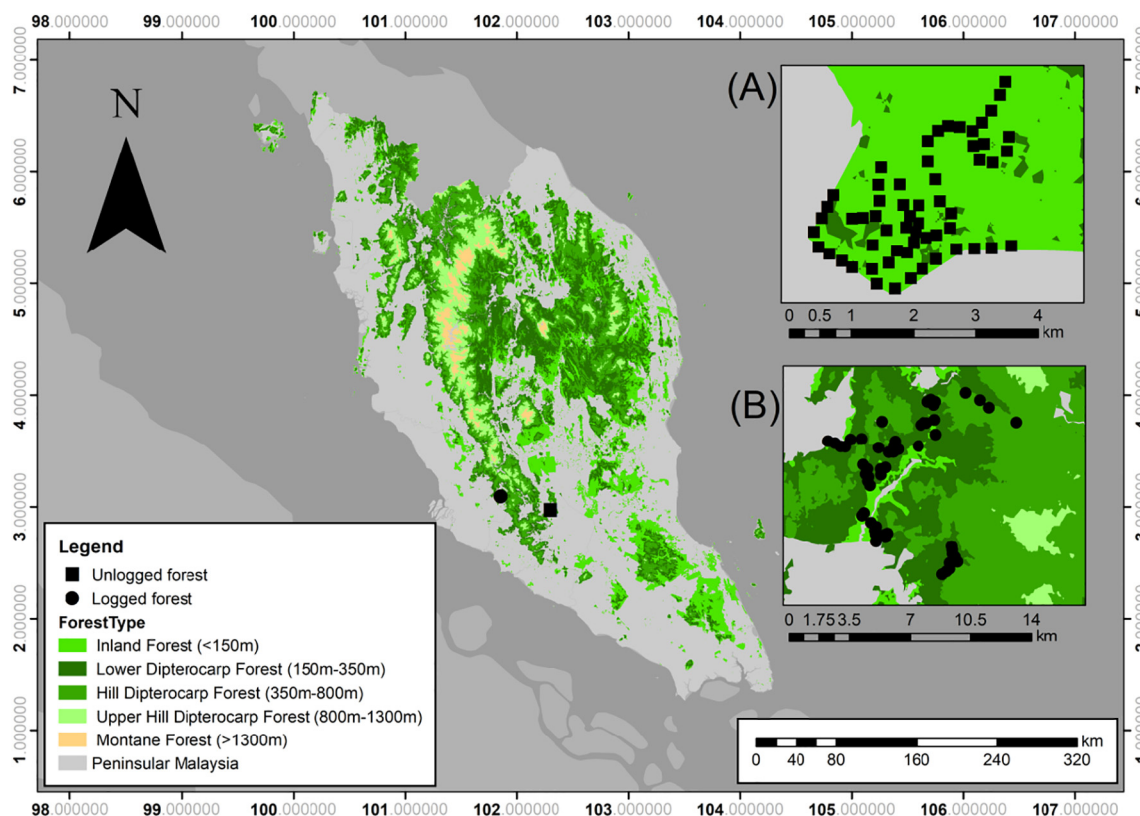


Fig. 1. Map of study areas showing the sampling plots in unlogged (A) and selectively logged (B) forests in Peninsular Malaysia.

**Table 1**  
Differences in habitat quality variables between logged and unlogged forests.

Variable	Mean $\pm$ SD		<i>t</i>	<i>p</i>
	Logged forest	Unlogged forest		
Trees with DBH > 45 cm	1.87 $\pm$ 1.41	3.23 $\pm$ 2.55	−3.56	< 0.001
Trees with DBH between 5 and 45 cm	31.10 $\pm$ 11.86	37.45 $\pm$ 18.31	−2.77	0.008
Bamboo abundance	1.12 $\pm$ 1.70	0	5.09	< 0.001
Palm abundance	3.78 $\pm$ 3.43	2.80 $\pm$ 3.14	1.59	0.117
Liana abundance	7.02 $\pm$ 4.99	9.20 $\pm$ 5.72	−2.06	0.044
Sapling abundance	12.22 $\pm$ 5.05	9.90 $\pm$ 5.57	2.36	0.022
Seedling abundance	7.83 $\pm$ 5.27	7.22 $\pm$ 5.43	0.63	0.533
Fallen tree abundance	1.37 $\pm$ 1.35	1.18 $\pm$ 1.07	0.89	0.378
Canopy cover (%)	91.20 $\pm$ 4.06	92.86 $\pm$ 4.33	−2.47	0.017
Altitude (m)	238.10 $\pm$ 80.27	132.10 $\pm$ 11.22	9.92	< 0.001

Korhonen and Heikkinen (2009). This script measures precisely and automatically the percentages of area covered with tree canopy and area with light or no tree canopy. Altitude was determined using the Garmin 78 GPS.

#### 2.4. Statistical analysis

We performed paired *t*-tests to compare habitat quality variables such as trees with DBH > 45 cm, trees with DBH between 5 and 45 cm, bamboo abundance, palm abundance, liana abundance, sapling abundance, seedling abundance, fallen tree abundance, canopy cover, and altitude between logged and unlogged forests. All the images captured by the camera traps were sorted and each animal image captured identified using a mammal guide written by Francis (2008). Blank and unclear images (< 1%) were excluded from the analysis and classified as unidentifiable species. We performed SIMPER analysis to assess the

contribution of each species to the observed similarity (or dissimilarity) between samples. We used the Bray-Curtis measure of similarity to compare each sample in the unlogged forest with each sample in the logged forest. The Bray-Curtis method operated at the species level, and therefore the mean similarity between forests could be computed for each species. We used ANOSIM analysis to test for differences in species composition at different locations. This was analysed by performing 999 permutations (random sample from a large number). Both SIMPER and ANOSIM were performed using PRIMER version 7.

We performed a two-sample Poisson test to compare mammal species richness between selectively the logged and unlogged forests. In addition, the number of animal images across all species was compared between selectively the logged and unlogged forests. We examined relationships between mammal species richness and stand- and landscape-level attributes using Generalized Linear Models (GLMs). To determine the key drivers of mammal species richness between species occurrence and habitat quality attributes, significant explanatory variables were determined using Wald's test. Correlation tests for multicollinearity among variables were conducted using global models that comprised all predictor variables. Since all explanatory variable pairs were not characterized by strong collinearity ( $r > 0.7$ ), none of the predictor variables were dropped from the global model (Dormann et al., 2013). We used all possible methods (i.e. fitting of all possible regression models) to select the final model. To determine models that might best reflect the underlying biological process, or spurious inclusion of senseless models, we selected data based on alternative hypotheses prior to data collection and analysis (Johnson and Omland, 2004).

We selected the most parsimonious models based on Mallows Cp values. Mallows Cp statistic has been used in multiple regression analysis to select models that contain smaller numbers of predictors from a larger number that is available for inclusion (Lance, 2014). Mallows Cp is likely to choose the same models as the Akaike information criterion (AIC) (Quinn and Keough, 2002). The criterion can be computed as

$\text{Dev} / f + 2 \times p - n$ , where Dev denotes the deviance of the current model,  $f$  denotes the dispersion parameter,  $p$  denotes the number of fitted parameters of the current model, and  $n$  denotes the number of units. Hence it does not include the null model. In addition, we reported the adjusted  $R^2$  for each candidate model. Mallows Cp is linked to the adjusted R-squared, but includes a heavier penalty for inflating the number of independent variables. Its values are generally positive and  $> 1$ , and lower values are better. The models which produce the best (lowest) values of Mallows Cp will likely to be comparable to those that yield the best (highest) values of adjusted R-squared. We provide graphs of the fitted model, which show the relationship of the response variable with each explanatory variable. All statistical analyses were conducted in GenStat version 15 (VSNi, Hemel Hempstead, UK).

### 3. Results

#### 3.1. General patterns of habitat quality and mammalian biodiversity

There were differences in vegetation structure characteristics between logged and unlogged forests apart from palm abundance, seedling abundance, and fallen tree abundance (Table 1). Trees with DBH  $> 45$  cm, trees with DBH between 5 and 45 cm, liana abundance, and canopy cover were significantly greater in unlogged forests compared to logged forests. In contrast, bamboo abundance and sapling abundance were significantly greater in logged forests compared to unlogged forests. A total of 3730 animal images were captured by the camera traps deployed across the forest study sites. From the images, 16 mammal species were identified (Table 2), with 16 species recorded in the unlogged forest and 10 species in the logged forest (Table 3). These include five conservation priority species: the Asian tapir (*Tapirus indicus*) and white-handed gibbon (*Hylobates lar*) are classified as ‘endangered’; the Malayan sun bear (*Helarctos malayanus*) and pig-tailed macaque (*Macaca nemestrina*) are classified as ‘vulnerable’; and the silvery lutung (*Trachypithecus cristatus*) is classified as ‘near threatened’. The remaining species captured are classified as least concern under the International Union for Conservation of Nature (IUCN) red list (Table 2). The most common species recorded in both forests were the long-tailed macaque (*Macaca fascicularis*), pig-tailed macaque (*M. nemestrina*) and Eurasian wild pig (*Sus scrofa*) (Table 3). We did not detect the presence of large-sized mammals including top carnivores and forest herbivores such as tigers, elephants, leopards and sambar deer in both logged and unlogged forests.

**Table 2**  
Conservation status of the recorded species in the study areas.

Common name	Scientific name	Family	IUCN red list
Asian tapir	<i>Tapirus indicus</i>	Tapiridae	Endangered
Malayan sun bear	<i>Helarctos malayanus</i>	Ursidae	Vulnerable
Barking deer,	<i>Muntiacus muntjak</i>	Cervidae	Least concern
Long-tailed macaque	<i>Macaca fascicularis</i>	Cercopithecidae	Least concern
Pig-tailed macaque	<i>Macaca nemestrina</i>	Cercopithecidae	Vulnerable
Silvery lutung	<i>Trachypithecus cristatus</i>	Cercopithecidae	Near threatened
Porcupine	<i>Hystrix brachyura</i>	Hystriidae	Least concern
White-handed gibbon	<i>Hylobates lar</i>	Hylobatidae	Endangered
Eurasian wild pig	<i>Sus scrofa</i>	Suidae	Least concern
Lesser mouse deer	<i>Tragulus javanicus</i>	Tragulidae	Least concern
Greater mouse deer	<i>Tragulus napu</i>	Tragulidae	Least concern
Common treeshrew	<i>Tupaia glis</i>	Tupaidae	Least concern
Polynesian rat	<i>Rattus exulans</i>	Muridae	Least concern
Malayan civet	<i>Viverra zibetha</i>	Viverridae	Least concern
Banded palm civet	<i>Hemigalus derbyanus</i>	Viverridae	Least concern
Leopard cat	<i>Prionailurus bengalensis</i>	Felidae	Least concern

#### 3.2. Comparison of mammal biodiversity between unlogged and logged forests

The species composition in the unlogged forest was different from the logged forest (ANOSIM: sample statistic,  $R = 0.436$ ;  $p = 0.01$ ). Our results revealed that mammal species richness was greater (Poisson test: normal approximation = 4.993;  $p < 0.001$ ) in unlogged forests (mean = 2.683 species per plot) compared to logged forests (mean = 1.383 species per plot) (Fig. 2). Similarly, unlogged forests (mean = 50.87 animal images per plot) had greater number of animal images (Poisson test: normal approximation = 45.468;  $p < 0.001$ ) than logged forests (mean = 6.43 animal images per plot) (Fig. 2). SIMPER analysis revealed similarity between unlogged and logged forests was generally very low. A pairwise similarity between the two forest types was 11.86%.

#### 3.3. Relationships between mammal species richness and habitat quality

Out of the 12 explanatory variables, we identified nine that were associated with mammal species richness. We found that mammal species richness increased with the abundances of trees with a DBH  $> 45$  cm, lianas, saplings and altitude (Fig. 3; Table 4). Mammal species richness was higher in wet months compared to dry months. In contrast, mammal species richness decreased with the abundances of bamboo, palms and seedlings (Fig. 3; Table 4). Species richness diminished at low altitude areas. The most parsimonious model with the lowest Mallows Cp (i.e. 1029.86) explained 21.64% of variation in mammal species richness across the sampling plots (Table 5).

### 4. Discussion

The unlogged forest had a higher mammalian species occurrence and a higher number of images captured compared with the logged forest. Our results are consistent with Magintan et al. (2017) who reported species abundance in unlogged forests was significantly greater than logged forests. Unlogged forests can harbour more species as it provides more nesting sites, greater food supply and lower human disturbances (Berry et al., 2010). The present study has a limitation with respect to sampling bias. Small species such as forest rats that would not normally be accurately captured by camera traps have also been included. Some of these (e.g. *Rattus exulans*) are presumably just rare because camera trapping is not a good way to sample them, rather than actually being rare in the habitat.

The explanatory variables that were significant and determine the number of mammalian species (number of trees with DBH  $> 45$  cm, lianas, number of bamboo clumps, number of saplings, and number of palm trees) are largely the result of forest gaps created due to human or natural activities occurring in both the unlogged and logged forests (Yamamoto, 2000; Sutrisno, 2009). The absence of large trees in these areas is likely to affect the persistence of forest mammal species (Adila et al., 2017) as they provide habitat and food resources to both the mammals and their prey.

Our data revealed that lianas and saplings were important determinants of mammal species richness. Selective logging normally operates by logging within selected stands until the cutting limit is fulfilled and the rest of the trees are retained. Tree felling promotes the creation of forest gaps, which initiates the growth of trees and saplings that become important food resources for herbivore species (McShea et al., 2009; Edwards et al., 2014). However, some gaps can facilitate the growth of fast growing plant groups such as climbing lianas, bamboos and palm trees (Edwards et al., 2014). Lianas have a significant ecological role in the forest, by suppressing tree recruitment and increasing tree mortality (Meijaard et al., 2005). However, lianas also provide valuable food sources for some animal species (Meijaard et al., 2005).

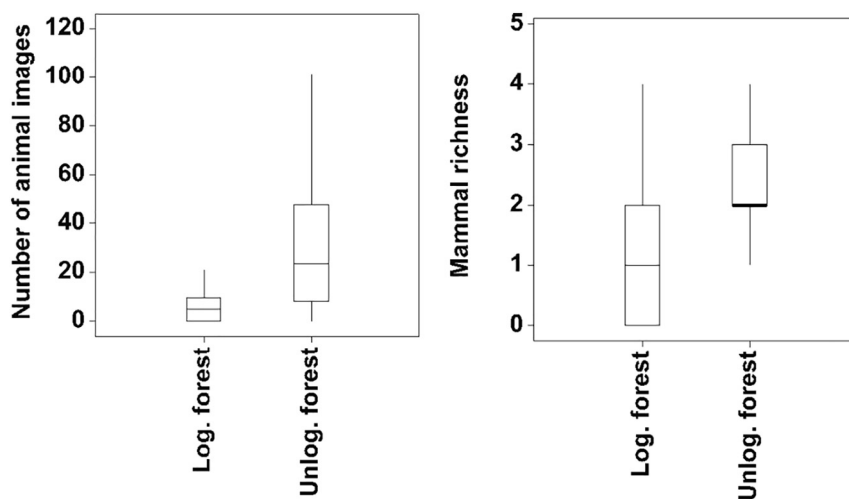
According to Coggins (2000) and Adila et al. (2017), a high number



**Table 3**

Average species abundance and relative contribution to total abundance in logged (average similarity = 17.44%) and unlogged (average similarity = 51.83%) forests, computed by SIMPER analysis.

Habitat	Species	Average abundance	Contribution (%)	Cum. contribution (%)
Logged forest	<i>Macaca fascicularis</i>	0.90	52.28	52.28
	<i>Sus scrofa</i>	1.01	37.49	89.76
	<i>Tupaia glis</i>	0.19	3.99	93.75
	<i>Muntiacus muntjac</i>	0.18	3.49	97.25
	<i>Tragulus javanicus</i>	0.12	0.94	98.19
	<i>Hystrix brachyura</i>	0.13	0.85	99.03
	<i>Rattus exulans</i>	0.07	0.73	99.77
	<i>Helarctos malayanus</i>	0.03	0.09	99.86
	<i>Tapirus indicus</i>	0.03	0.08	99.94
	<i>Hylobates lar</i>	0.04	0.06	100.0
Unlogged forest	<i>Macaca nemestrina</i>	4.47	58.50	58.50
	<i>Sus scrofa</i>	2.99	39.60	98.10
	<i>Tapirus indicus</i>	0.30	1.08	99.17
	<i>Tupaia glis</i>	0.29	0.64	99.81
	<i>Rattus exulans</i>	0.15	0.11	99.92
	<i>Tragulus napu</i>	0.07	0.04	99.96
	<i>Tragulus javanicus</i>	0.09	0.03	99.99
	<i>Viverra zibetha</i>	0.06	0.01	99.99
	<i>Prionailurus bengalensis</i>	0.03	0.01	100.00
	<i>Helarctos malayanus</i>	0.00	0.00	100.00
	<i>Muntiacus muntjak</i>	0.02	0.00	100.00
	<i>Macaca fascicularis</i>	0.00	0.00	100.00
	<i>Trachypithecus cristatus</i>	0.00	0.00	100.00
	<i>Hystrix brachyura</i>	0.00	0.00	100.00
	<i>Hylobates lar</i>	0.00	0.00	100.00
	<i>Hemigalus derbyanus</i>	0.02	0.00	100.00



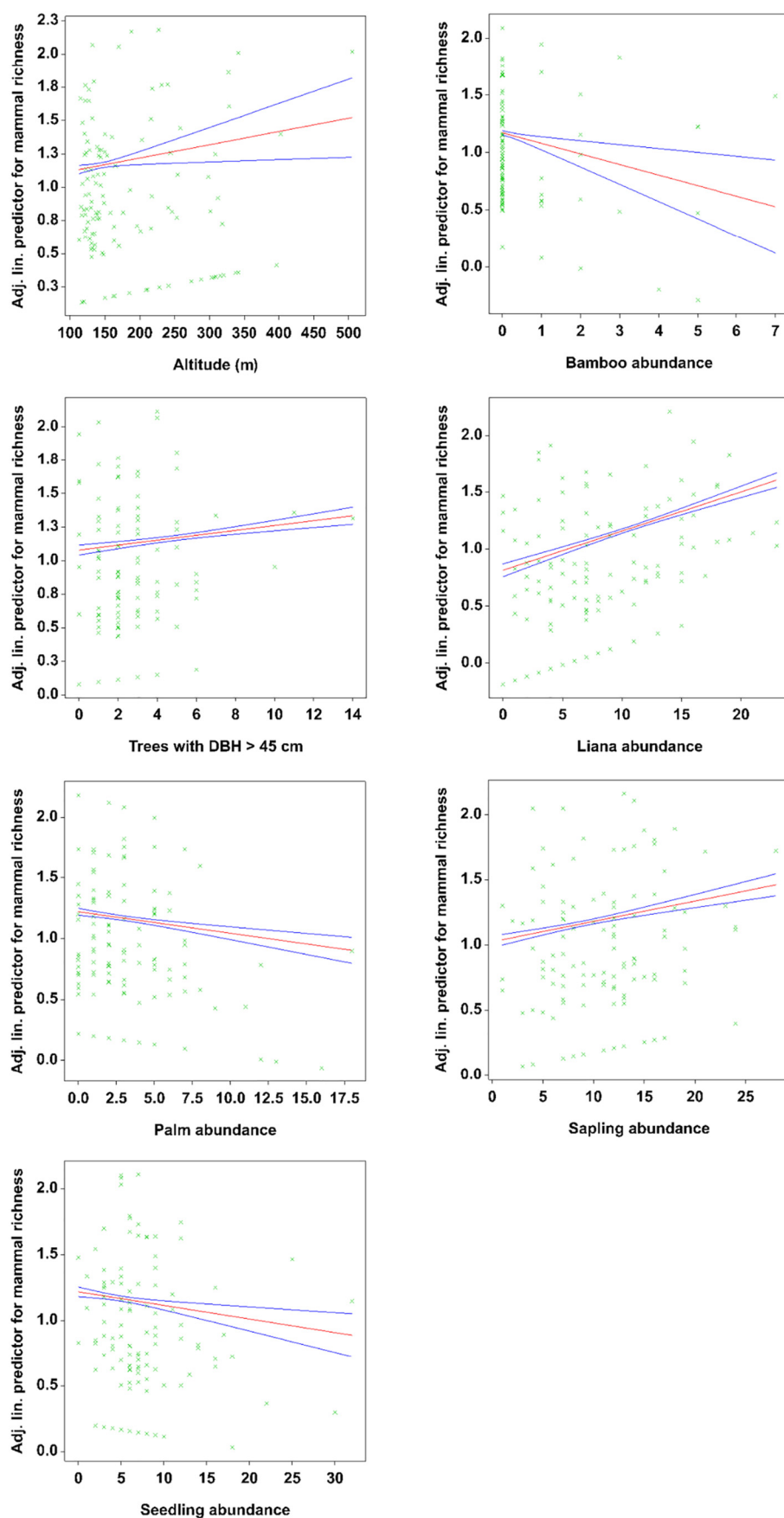
**Fig. 2.** Boxplots showing number of animal images and mammal species richness in selectively logged and unlogged forests. The bottom and top of the box are the first and third quartiles, and the band inside the box is the median (the second quartile). The whiskers represent the extreme values (the locations of the minimum and maximum).

of palm trees and bamboo clumps may result in decreased mammal species occurrence in logged forests. Medium to large sized mammals are likely to take wider forest trails instead of pathways that are full of obstacles (Bernard et al., 2013; Mohamed et al., 2013) such as bamboo clumps and palms. Additionally, Griscom and Ashton (2003) pointed out that the presence of bamboo stunts the growth rate and survival of trees, causing slow forest succession. Consequently, this could reduce the number of saplings. In our study bamboo clumps were more abundant in the logged forest than in the unlogged forest. This finding is similar to a study conducted by Larpkern et al. (2011), which stated that bamboo canopies and their litter affect sapling growth, leading to high abundance of bamboos in a logged forest.

Selective logging may cause the loss of important habitats, yet, increased browsing availability for terrestrial ungulates, thereby indirectly benefiting large carnivores (Linkie et al., 2008). However, the absence of top carnivores (e.g. *Panthera tigris* and *Panthera pardus*) in our study indicates that selective logging is not compatible with the conservation of large carnivores. Surprisingly, top carnivores as well as

other large-sized mammals were also absent in the unlogged forest. This may indicate that the negative effects of selective logging may not be limited to designated logging concession areas, but the ecological effects can extend into unaffected areas. Although abundant food can boost carnivore populations, populations are negatively affected by habitat fragmentation and hunting (Meijaard et al., 2005; Linkie et al., 2008). Besides that, anthropogenic threats may originate from the nearby oil palm plantations. Hunting impacts on wildlife can be exacerbated by the expansion of oil palm plantations if poachers enter forests via the plantations (Azhar et al., 2012, 2014). With respect to civets, our data are consistent with Heydon and Bulloh (1996) which reported that *Viverra zibetha* and *Hemigalus derbyanus* abundances decrease after logging.

In contrast to large carnivores small forest ungulates can tolerate logging by utilising a mix of fruits, forest and non-forest plants (Meijaard et al., 2005). The herbivore species found in this study, *Muntiacus muntjak*, *Tapirus indicus*, *Hystrix brachyura*, *Tragulus javanicus* and *Tragulus napu*. *Tragulus* sp. have all been found to be more common



**Fig. 3.** Scatterplots with regression (red) line and 95% confidence intervals (blue line) showing the relationships between the mammal species richness and habitat quality characteristics. By default for GLMs, the fitted relationship is plotted on the original scale, but the option to use the scale of the linear predictor was selected to check for potential non-linearity in the response. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 4**

GLMs of responses of mammal species richness to significant habitat quality variables.

Explanatory variable	df	Slope	s.e.
Trees with DBH > 45 cm	1	0.01455	0.00356
Bamboo abundance	1	−0.0961	0.0300
Palm abundance	1	−0.01584	0.00361
Liana abundance	1	0.03310	0.00256
Sapling abundance	1	0.01570	0.00223
Seedling abundance	1	−0.00874	0.00310
Altitude (m)	1	0.001168	0.000417
Forest type (unlogged forest)	1	0.3149	0.0580
Season (wet month)	1	0.1125	0.0323

**Table 5**Best subsets from candidate models. The most parsimonious model (labelled with \*) has six explanatory variables with the lowest Mallow Cp and a relatively high adjusted R<sup>2</sup>.

Best subsets with n term(s)	Explanatory variable	Mallows Cp	Adjusted R <sup>2</sup>
1	Liana abundance	1273.73	10.74
2	Model 1 + trees with DBH > 45 cm	1169.50	16.91
3	Model 2 + forest type	1120.51	19.50
4	Model 3 + sapling abundance	1085.88	21.16
5	Model 4 + palm abundance	1059.83	22.27
6	Model 5 + season	1045.11	22.62
7	Model 6 + bamboo abundance	1039.07	22.37
8	Model 7 + seedling abundance	1034.97	21.97
9	Model 8 + altitude*	1029.86	21.64
10	Model 9 + canopy cover	1031.45	20.82
11	Model 10 + trees with DBH between 5 and 45 cm	1033.42	19.95
12	Model 11 + fallen tree abundance	1035.42	19.06

in the logged forest than in mature forests in Peninsular Malaysia (Johns, 1997). Unlogged forests are characterized by a high level of vegetation complexity that provides a heterogeneous wildlife habitat and increases biodiversity, particularly of species that rely on large, mature trees (Nowell and Jackson, 1996; Azlan and Sharma, 2006). Our findings show that logged forests did not recover to pre-harvest levels of biodiversity, even after several decades.

Logged forest has lower mammalian species richness due to a range of anthropogenic factors such as agricultural expansion, poaching, and illegal logging (Brookfield and Byron, 1990; McMorro and Talip, 2001; McShea et al., 2009; Burivalova et al., 2014). Bernard et al. (2014) suggested that mammals which utilise logged forest are well adapted and can survive in highly modified habitats. Our study found common species such as *Macaca fascicularis* and *Sus scrofa* frequently in the logged forest. Mammals such these may exploit the food resources in open and disturbed areas, whereas other species will avoid these areas (Rickart et al., 2011).

Primates such as *Macaca fascicularis* and *Macaca nemestrina*, which are generalist feeders, seem fairly adaptable to selective logging and are able to change ranging patterns and diets in response to modifications in forest structure and composition (Johns, 1997). The decrease in mammalian species diversity in logged forest compared to unlogged forest is likely to result in increased risk of local extinction or poor distribution of mammals in these areas.

Wet months seem to be the best season to conduct inventory surveys with camera traps in the study areas. Higher species richness during the wet months indicates frequent movements by mammals to search for the more sparse food resources. Cusack et al. (2015) reported that larger bodied species were more likely to be detected during the wet season.

## 5. Conclusion

This study showed that unlogged forest had greater species richness compared with the logged forest and identified the key vegetation structural characteristics that were associated with those differences. The absence of large-sized mammals in both selectively logged and unlogged forests is a major concern that requires serious attention and revision of the current forest management system in Peninsular Malaysia. There is a need for all stakeholders involved in forest management to undertake habitat restoration programmes to improve landscape connectivity between selectively logged and unlogged forests. In addition, the remaining unlogged lowland dipterocarp forests should be protected to safeguard the current mammalian biodiversity in the region. Conservation agencies have to take necessary measures (e.g. law-enforcement patrol) to tackle wildlife poaching in both logged and unlogged forests. Where selective logging occurs, foresters need to seriously consider adopting RIL to reduce negative impacts on mammalian biodiversity. Further research should be undertaken on individual species of forest mammals to provide a better understanding of the long-term effects of selective logging in Southeast Asia. This information is essential to develop successful policy guidelines for managing tropical forestry landscapes.

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