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Authors: Nurfatin Adila, Selvadurai Sasidhran, Norizah Kamarudin, Chong Leong Puan, Badrul Azhar, David B. Lindenmayer

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Effects of peat swamp logging and agricultural expansion on species richness of native mammals in Peninsular Malaysia

Nurfatin Adila[1], Selvadurai Sasidhran[1,2], Norizah Kamarudin[1], Chong Leong Puan[1], Badrul Azhar[1,3], David B. Lindenmayer[4]

[1]Department of Forest Management, Faculty of Forestry, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia

[2]WWF Malaysia, 1 Jalan PJS 5/28A, Petaling Jaya Commercial Centre (PJCC), 46150 Petaling Jaya, Selangor, Malaysia

[3]Biodiversity Unit, Institute of Bioscience, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia

[4]The Fenner School of Environment and Society, ANU College of Medicine, Biology and Environment, Australian National University, Canberra ACT 0200, Australia

Corresponding author. E-mail address: b_azhar@upm.edu.my (B. Azhar), telephone (Office): +60389467206, fax: +60389432514.

Abstract

The biodiversity inhabiting tropical peat swamp forests in Southeast Asia is currently threatened by commercial logging and agricultural expansion. The occurrence of mammals in such forests is often poorly known and the factors influencing their occurrence in these ecosystems have rarely been quantified. We aim to determine the key habitat and landscape drivers of mammal species richness in fragmented peat swamp reserves. We conducted camera trap surveys in the North Selangor Peat Swamp Forest (NSPSF), the last remaining area of peat swamp forest on the west coast of Peninsular Malaysia. We also measured vegetation structure and landscape metrics to investigate the relationship between these factors and mammal richness. We recorded a total of

16 mammal species from 45 sampling sites using camera traps located in peat swamp forest reserves. Mammal species richness increased with the abundance of large trees and distance away from roads. Species richness decreased significantly with canopy cover and height, the abundance of fallen trees, the abundance of forest palms and saplings, distance away from rivers, and a measure of landscape compositional heterogeneity. Our findings underscore the high conservation value of logged peat swamp forests and the urgent need to halt further deforestation. We recommend: (1) protecting riparian habitat; (2) avoiding further forest conversion particularly areas supporting large trees into oil palm plantations; and (3) limiting road development within and around the NSPSF.

Keywords: Biodiversity; camera trap; oil palm; forest

Introduction

Tropical peat swamp forest in Southeast Asia covers 25 million hectares and is globally important for biodiversity conservation (Parish *et al*. 2014). The annual loss of approximately 5.2 million hectares of tropical forests worldwide between 2000 and 2010 including those in Southeast Asia (FAO 2010) has adversely affected more than 50% of vertebrate animal species, particularly forest taxa (Brooks *et al*. 2002; Wilcove *et al*. 2013). Southeast Asia's tropical peat swamp forests are under enormous threat from logging, fire, habitat fragmentation, and land conversion to establish oil palm plantations and smallholdings. However, the value of the peat swamp forest ecosystem for biodiversity remains poorly understood (Sheil *et al*. 2009; Sodhi *et al*. 2010; Koh *et al*. 2011; Miettinen *et al*. 2011a, 2011b; Posa *et al*. 2011).

Previous studies have indicated that tropical peat swamp forests are important habitat for mammals (Morrogh-Bernard *et al*. 2003; Felton *et al*. 2003; Cheyne *et al*. 2010, 2011). However, mammals in peat swamp forests are understudied compared to those in other forest types such as lowland and hill dipterocarp forests (Posa *et al*. 2011). This is an important knowledge gap because actions to promote the conservation of species depends on understanding where species occur as well as the quantification of the factors influencing why they occur where they do (Mackey et al., 2001; Elith *et al*. 2009). We addressed this knowledge gap in this study through an intensive camera trap study of the mammal fauna in the North Selangor Peat Swamp Forest (NSPSF) located in west coast of Peninsular Malaysia. This area is one of the most important and largest remaining peat swamp forests of its kind (Azhar *et al*. 2011).

To date, camera trap-based sampling has not been conducted to investigate the diversity and habitat preferences of wildlife species in the NSPSF. Prentice and Aikanathan (1989) reported the presence of 20 mammal species in the NSPSF including the Sumatran Rhinoceros (*Dicerorhinus sumatrensis*) and Malayan Tiger (*Panthera tigris*). Their surveys were based on sightings and tracks as well as indirectly through information from local inhabitants (e.g. loggers, farmers and fishermen), and revealed that the Asian Elephant (*Elephas maximus*) was locally extinct in the NSPSF at that time (Prentice & Aikanathan 1989).

We gathered baseline data on mammal species richness, with the exception of small rodents and bats, in the NSPSF and quantified the influence on species richness of multiple anthropogenic factors such as past logging activities, forest fragmentation, and oil palm expansion. We also quantified relationships between mammal species richness and local-level factors. The results of this study are important to determine which species occur in the NSPF and where they occur.

Knowledge of faunal biodiversity in tropical peat swamp forests is far from complete and these forests are disappearing rapidly (Yule 2010). Given that tropical peat swamp forests are more vulnerable than other forest ecosystems in Southeast Asia, protecting the forests and peat swamp biodiversity are conservation priorities that require urgent action (Posa *et al*. 2011).

Methodology

Study site

We conducted this study at the North Selangor Peat Swamp Forest (NSPSF) (between 3°40'26.56"N, 101°4'29.52"E and 3°32'4.40"N, 101°27'33.36"E), situated in the state of Selangor, on the west coast of Peninsular Malaysia (Figure 1). The forest covers 81,304 ha and comprises three forest reserves, namely Raja Musa Forest Reserve (36,938 ha), Sungai Karang Forest Reserve (36,654 ha), Sungai Dusun Wildlife Reserve (4,891 ha), and part of the Bukit Belata extension (2,821 ha) (Parish *et al*. 2014). The local climate is characterized by heavy rainfall and high humidity and temperature. Mean temperature is 27 °C and the mean relative humidity is 79.3% (Malaysian Meteorology Department 2015). The vegetation in NSPSF includes common tree species such as *Macaranga pruinosa*, *Campnosperma coriaceum, Pternandra galeata* and *Shorea platycarpa* (Yule & Gomez 2009), the ferns *Stenoclaena palustris, Asplenium longissimum, Nephrolepsis biserrata* and sedges: *Cyperus rotundus* and *Pandanus artocarpus* (Yule & Gomez 2009).

Logging operations in the NSPF ceased in the early 1990s (Azhar *et al*. 2011). The cutting limit prescribed in the NSPSF for both mature dipterocarp and non-dipterocarp trees ranged from 50 cm to 70 cm diameter at breast height (DBH), with maximum volume allowed to be harvested set at 85 m^3 per ha (Forestry Department 1997). Historically, timber was shipped from the forest using rivers or human-constructed canals.

The NSPSF is surrounded by oil palm plantations and smallholdings, rice fields, and human settlements (Azhar *et al*. 2011). Apart from being threatened by the expansion of oil palm plantations, forest fires also occur frequently, especially during severe dry seasons (Parish *et al*. 2014). At the national level, this forest has yet to be designated as a protected area (Kumari 1995; Parish *et al*. 2014). Forest conversion occurred during the current survey with 370 ha of peat swamp forest being cleared between 2012 and 2015 to establish an oil palm plantation in the north-eastern part of the NSPSF. This was despite the affected area being part of forest reserve.

Sampling design and camera trapping

We were granted permission from the Selangor Forestry Department to conduct this study in the NSPSF. Our use of camera traps was approved by the Department of Wildlife and National Parks. Because the sampling method is non-intrusive, our research did not require approval from an animal ethics committee. We established camera traps at 45 sampling sites in the NSPSF (Figure 1). We selected camera-trap placements on the basis of the potential suitability of a given area for mammals using visible animal trails, footprints, scats and tree markings (Karanth & Nichols 1998). Although forest trails are known to be travelled by some mammal species (Bernard *et al*. 2013; Mohamed *et al*. 2013), we avoided those trails with a sign of human encroachment (e.g. rubbish and camping sites). Cameras were set 0.5 m above the ground and attached to suitable trees (Ancrenaz *et al*. 2012). The furthest distance between sites was 40 km and the nearest was 500 m. The precise location of each camera trap was confirmed using a handheld Global Positioning System (GPS) (Garmin 72H).

We deployed cameras from May 2013 until October 2014. We used 21 passive infrared (PIR) camera traps (Bushnell Trophy Cam and Bushnell Trophy Cam HD [Bushnell Outdoor Products, Overland Park, Kansas, USA]). Each camera was programmed with an 8.0 megapixel HD model mode with three images per shot within a one-second interval. The cameras were left in place for two months at each site. To replace battery cells and retrieve images, we conducted monthly maintenance on the cameras.

Local-level and landscape-level factors

We measured or calculated a range of attributes at each sampling site and used them as potential explanatory variables in models of mammal species richness (Table 1). Local-level factors included: (1) number of saplings with diameter at breast height (DBH) of 1-5 cm; (2) number of trees with DBH more than 30 cm; (3) number of palms (e.g. *Eugeissona tristis* and *Licuala grandis*); (4) number of fallen trees with DBH than 30 cm; (5) canopy cover determined using densitometer; and (6) canopy height measured using a laser rangefinder. Vegetation plots of 20 m x 50 m were established at the camera trap site. Cameras were deployed in the middle of each plot.

Three landscape attributes were calculated using measuring tools in Google Earth Pro (Version 6.0) (Table 1): (1) distance to nearest large river from the camera-trapping site; (2) distance to nearest road; and (3) landscape compositional heterogeneity within a 1 km radius (i.e. a total of six different kinds of land cover or land use such as peat swamp forest, large-scale oil palm plantation, small-scale oil palm farm or smallholding, rice field, secondary non-forest vegetation, and open area). This was based on geometrical shape, size, context, and pattern of different land uses (Horning *et al*. 2010). Visual interpretation and landscape measurements were made using the most recent satellite or aerial images in Google Earth Pro (Azhar *et al*. 2015). To avoid images with high level of cloud cover, we utilized the historical imagery feature in Google Earth Pro for visual interpretation (Azhar *et al*. 2015).

Data analysis

We quantified relationships between mammal species richness and local- and landscape-level attributes using Generalized Linear Models (GLMs). Two models were developed separately to determine the potential key drivers of mammal species richness. The first model was for local-level attributes and the second model was for landscape-level attributes. Species richness was defined as the total number of species detected at each site over the 18-month duration of the study. There were insufficient records to facilitate modelling of the factors influencing the occurrence of individual species of mammals. Correlation tests for multicollinearity among variables were conducted in the global models which comprised all predictor variables. Predictor variables characterized by strong collinearity ($r > 0.7$) were dropped from the subsequent model (Dormann *et al*. 2013). However, none of the predictor variables was removed from the global models as all variables had been confirmed to be independent. We conducted modelling using a Poisson distribution and logarithm link function. Of 13 predictor variables, 11 variables were included in the models.

To identify the most parsimonious model, we used an information theoretic (IT) approach (Burnham & Anderson 2002). We selected the best model from a collection of candidate models based on the minimum Akaike's Information Criterion (AIC) values and then computed the AIC weights (Burnham & Anderson 2002). Because sample size (n), relative to parameters (K), was not large (n/K < 40) for at least one of the models (sample size, n = 45), we used a corrected AIC (AICc) to compare the models (Burnham & Anderson 2002). The use of AIC_C reduced the probability of overfitting models (Burnham & Anderson 2002). We reported R^2 values for each model to complement the AIC value. The candidate models were selected from all possible combinations of all parameters, which were then fitted to the data and ranked by ΔAICc values (AICc - AICcmin). We reported the top models that include all models with ΔAICc values < 2, as well as those with ΔAICc > 2 (Gardner et al. 2016). All statistical analyses were conducted in GenStat version 15 (VSNI, Hemel Hempstead, UK).

Results

Overall species richness

We captured a total of 5,046 images from 2,565 trap nights of camera surveys. We excluded photos that were not clear, leaving 4,997 images for species identification. We recorded a total of 16 mammal species ($\bar{x} \pm$ S.E. = 2.8 ± 0.259 species per site; range: 0-6 species per site) (Table 2, Figure 2); of which five were herbivores, four were carnivores, and eight were omnivores. One of the species we recorded, Asian Tapir (*Tapirus indicus*) is listed as Endangered by the IUCN Red List (IUCN, 2014). Three species, the Malayan Sun Bear (*Helarctos malayanus*), Bearded Pig (*Sus barbatus*), and Pig-tailed Macaque (*Macaca nemestrina*) are listed as Vulnerable. White-tighed Surii (*Presbytis siamensis*), Black Panther (*Panthera pardus*) and Large Indian Civet (*Viverra zibetha*) are classified as Near Threatened, while the remaining nine species are classified as Least Concern in the IUCN Red List (IUCN, 2014).

Local-level effects of vegetation structure

The final model for overall mammal species richness includes the following six variables (AIC = 1220.3, AICc = 1222.5; R^2 = 41.63%) (Table 3): canopy cover and height; fallen trees with DBH greater than 30 cm; number of forest palms; number of saplings; and trees with DBH more than 30 cm. Overall species richness increased with abundance of trees with DBH more than 30 cm (slope = 7.929×10^{-3}) (Figure 3). Overall species richness decreased significantly with canopy cover (slope = -1.754×10^{-3}), fallen tree with DBH greater than 30 cm (slope = -0.06066), canopy height (slope = -0.05746), the abundance of forest palms (slope = -0.01924), and the abundance of saplings (slope = -4.752×10^{-3}) (Figure 3). This model accounted for 100% of the Akaike weights in the model set (Table 3).

Landscape-level effects of rivers, roads and compositional heterogeneity

The most parsimonious model for overall mammal species richness includes the following three variables (AIC = 1550.7, AICc = 1551.29; R^2 = 25.11%) (Table 3): landscape compositional heterogeneity, distance from nearest large river; and distance from nearest road. Overall species richness increased with distance away from roads (slope = 0.02871) (Figure 3). Overall species richness decreased significantly with distance from large rivers (slope = -0.06096) and the compositional heterogeneity (slope = -0.03097) (Figure 3). This model accounted for 99.6% of the Akaike weights in the model set (Table 3).

Discussion

Our research fills an important knowledge gap about the biota remaining in the NPSF. We recorded the Endangered Asian Tapir in the NSPSF, but our cameras did not capture images of the Critically Endangered Sumatran Rhinoceros (*Dicerorhinus sumatrensis*). Its last known sighting was made in the same peat swamp forests was in 1994 (Tan, 2013). We recorded the rare Bearded Pig (*Sus barbatus*), in the NSPSF. We found that the wild boar was the most commonly recorded species in the reserves. The prevalence of this species maybe associated with the absence of large predators (e.g. tigers) in the area and the availability of food in the adjacent oil palm plantations (Ickes 2001). Prentice and Aikanathan (1989) reported no sighting of Malayan Tiger (*Panthera tigris*) during their survey, although a tiger was sighted by logging workers five years earlier in the NSPSF. Of five primate species recorded by Prentice and Aikanathan (1989), we recorded only three species (Table 1). Although the Lar Gibbon (*Hylobates lar*) was not recorded by the camera traps, we detected shouting calls made by this species while deploying cameras for this survey.

We have completed a major camera-based survey of mammals in the NSPSF. The only other large-scale survey of the same area was made 25 years ago by Prentice and Aikanathan (1989). They gathered data over a year using local knowledge, animal tracks, and sightings. Using these methods, Prentice and Aikanathan (1989) recorded 13 mammal species that we did not detect: Sambar Deer (*Cervus unicolor*); Pangolin (*Manis javanica*); Binturong (*Arctictis binturong*); Otter (*Lutra* sp.); five squirrel species (Family Sciuridae); two treeshrew species (Family Tupaiidae); and Large Flying Fox (*Pteropus vampyrus*). In contrast, Prentice and Aikanathan, (1989) did not record at least six species detected in our camera trapping. These were Bearded Pig (*Sus barbatus*), Large Indian Civet (*Viverra zibetha*), Greater Mousedeer (*Tragulus napu*), Leopard Cat (*Prionailurus bengalensis*), Small Asian Mongoose (*Herpestes javanicus*), and Malayan Porcupine (*Hystrix brachyura*).

Our results suggest that levels of mammal biodiversity maybe depleted in areas close to roads (Azhar *et al*. 2013; Clements *et al*. 2014). Roads can have adverse effects on biota through habitat fragmentation and vehicle collisions (Benitez-Lopez *et al*. 2010; Taylor & Goldingray 2010). Tropical species are especially vulnerable to roads as many specialists avoid clearings and forest edges associated with road construction (Laurance *et al*. 2009). Other species are susceptible to becoming road kill, or to predation or hunting by humans using roads (Taylor & Goldingray 2010).

Our results indicate that mammal species richness decreased with landscape compositional heterogeneity. Existing studies have suggested that increasing the compositional heterogeneity in human-modified landscapes may improve biodiversity conservation (Fahrig *et al*. 2011; Steckel *et al*. 2014; Azhar *et al*. 2015). We suggest that this may be an outcome of a small number of wild animals using resources from both peat swamp forests and adjacent agricultural areas. Some wildlife species such as the wild boar and Asian Tapir may use oil palm plantations around the NSPSF, because a wide variety of food sources are available in the ecotone between these two kinds of areas (Normua *et al*. 2004; Maddox *et al*. 2007; Azhar *et al*. 2013, 2014; Meijaard & Sheil 2013; Jennings *et al*.

2015). Large mammals often have a large home range (Wong *et al*. 2004; Linkie *et al*. 2013) which may include agricultural lands. Previous studies on the sun bear and felids also suggested that their home ranges can include oil palm plantations (Azlan *et al*. 2006; Maddox *et al*. 2007; Azhar *et al*. 2014; Jennings *et al*. 2015). However, human-wildlife conflict (e.g. crop raiding and livestock predation) may occur along the boundaries between oil palm areas and peat swamp forest (Ickes 2001; Linkie *et al*. 2006; Maddox *et al*. 2007; Marchal *et al*. 2009; Ramirez & Simonetti 2011; Wong & Linkie 2013).

We found that the abundance of trees with a DBH exceeding 30 cm influenced mammal species richness. Some species of mammals favor larger trees where they move under forest canopy to forage in dense vegetation (Gutierrez *et al*. 1997; Monamy & Fox 2000) or to hide from predators (Garden *et al*. 2007; Douglas *et al*. 2009; Schaub *et al*. 2010; Fuentes-Montemayor *et al*. 2013). The results of this study also demonstrate that the relationship between mammal species richness increased with the abundance of trees with a DBH less than 45 cm. Available data indicate that the tree communities in the NSPSF are important to the persistence of forest species in tropical, human-modified landscapes.

Our results revealed that mammal species richness decreased with the canopy height and cover. A low level of mammal species richness may also be attributed to high abundance of saplings and forest palms. These factors suggest that mammal habitat suitability in the NSPSF may still be recovering from past logging. Logged and regenerated areas support fast growing and light-demanding plant species such as *Macaranga* spp. in the NSPSF ($\bar{x} \pm SE = 12.53 \pm 1.479$ trees per site; range = 0-41 trees). Only a small number of the larger, commercial timber trees with a DBH of more than 30 cm remain in the NSPSF ($\bar{x} \pm SE = 1.489 \pm 0.296$ trees per site; range = 0-8 trees). Thus, the canopy height ($\bar{x} \pm SE = 11.70 \pm 0.272$ m per site; range = 6.916.9 m) was dominated by the fast-growing and light-demanding species that are presently of limited habitat value for mammal species.

We found that mammal species richness was higher close to large rivers. Large wild animals may be attracted to riparian habitats that provide feeding and nesting resources (Naiman & Rogers 1997). Although terrestrial habitats adjacent to rivers have less forest cover, these riparian habitats may provide important key food sources for terrestrial mammals such as ungulates and primates (Lees

& Peres 2008). River banks in the NSPSF are also subject to frequent natural disturbances (e.g. herbivory, fire, and seasonal flooding) resulting in relatively heterogeneous and complex microhabitat conditions (Olson *et al*. 2007) which support diverse faunal groups. The use of terrestrial habitats adjacent to rivers or streams by a broad range of taxa, including mammals, birds, reptiles, and amphibians has been reported in a number of studies (McComb *et al*. 1993; Darveau *et al*. 1995, 2001; Hodges & Krementz 1996; Bodie 2001; Semlitsch & Bodie 2003).

Conservation implications

Forest loss due to anthropogenic factors poses a critical threat to mammals with large home ranges (Wong *et al*. 2004; Linkie *et al*. 2003; Rayan & Linkie 2015). The NSPSF is being threatened by oil palm expansion, cattle farming, poaching and forest fire (Sasidhran *et al*. 2016). We emphasize the importance of developing a systematic, long-term repeated survey approach to appropriately monitor the long-term occurrence and persistence of species within NSPSF. This is particularly critical given the importance of this area as the largest remaining forest of its type in Peninsular Malaysia. Conservation agencies must strengthen current natural habitat protection strategies to prevent local extinction of threatened large mammals, particularly top predators and high conservation value species. These strategies should include: (1) protecting areas near rivers as this is where the most mammals occur; (2) avoiding further forest conversion to oil palm monocultures, particularly areas supporting bigger trees; and (3) minimizing the construction of roads in and around the NSPSF.

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Figure 1. Map of study area. (a) Location of study area in Selangor, Peninsular Malaysia; (b) Location of sampling sites; (c) Deforestation in the NSPSF to establish 370 ha of oil palm monocultures in 2013.

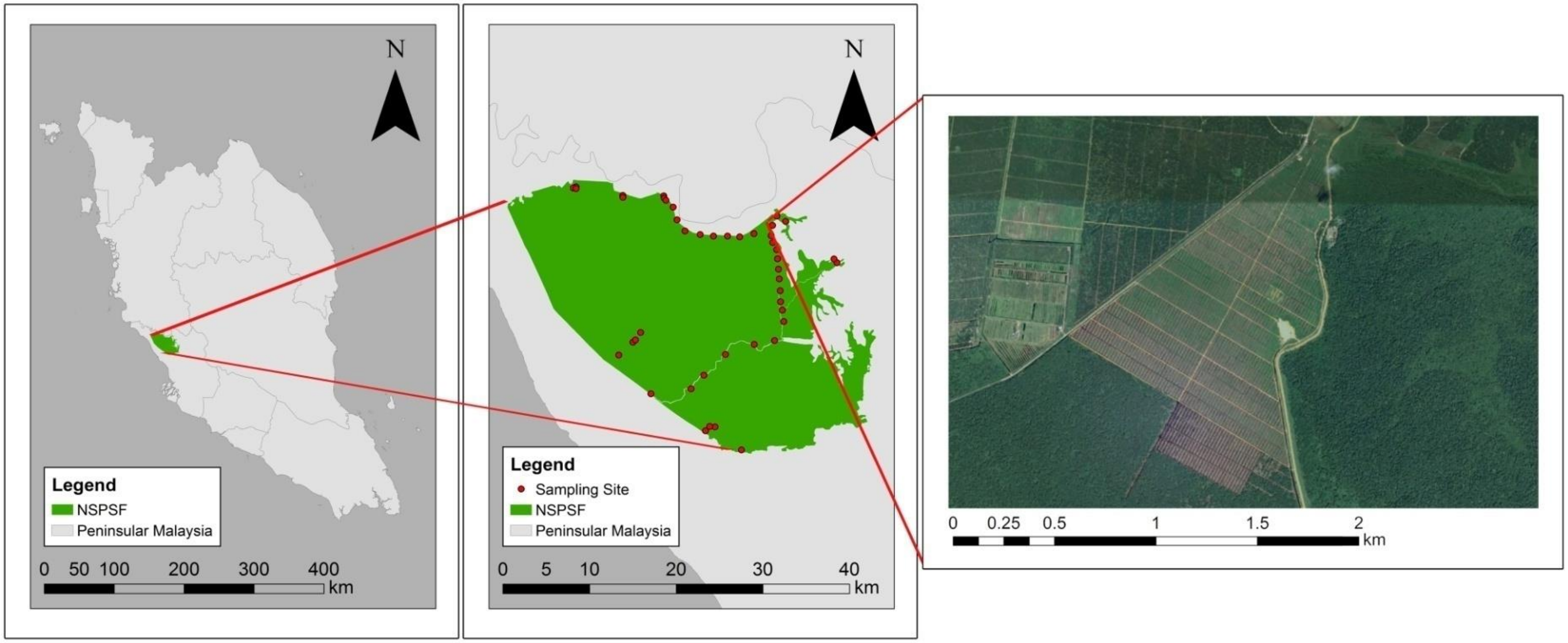
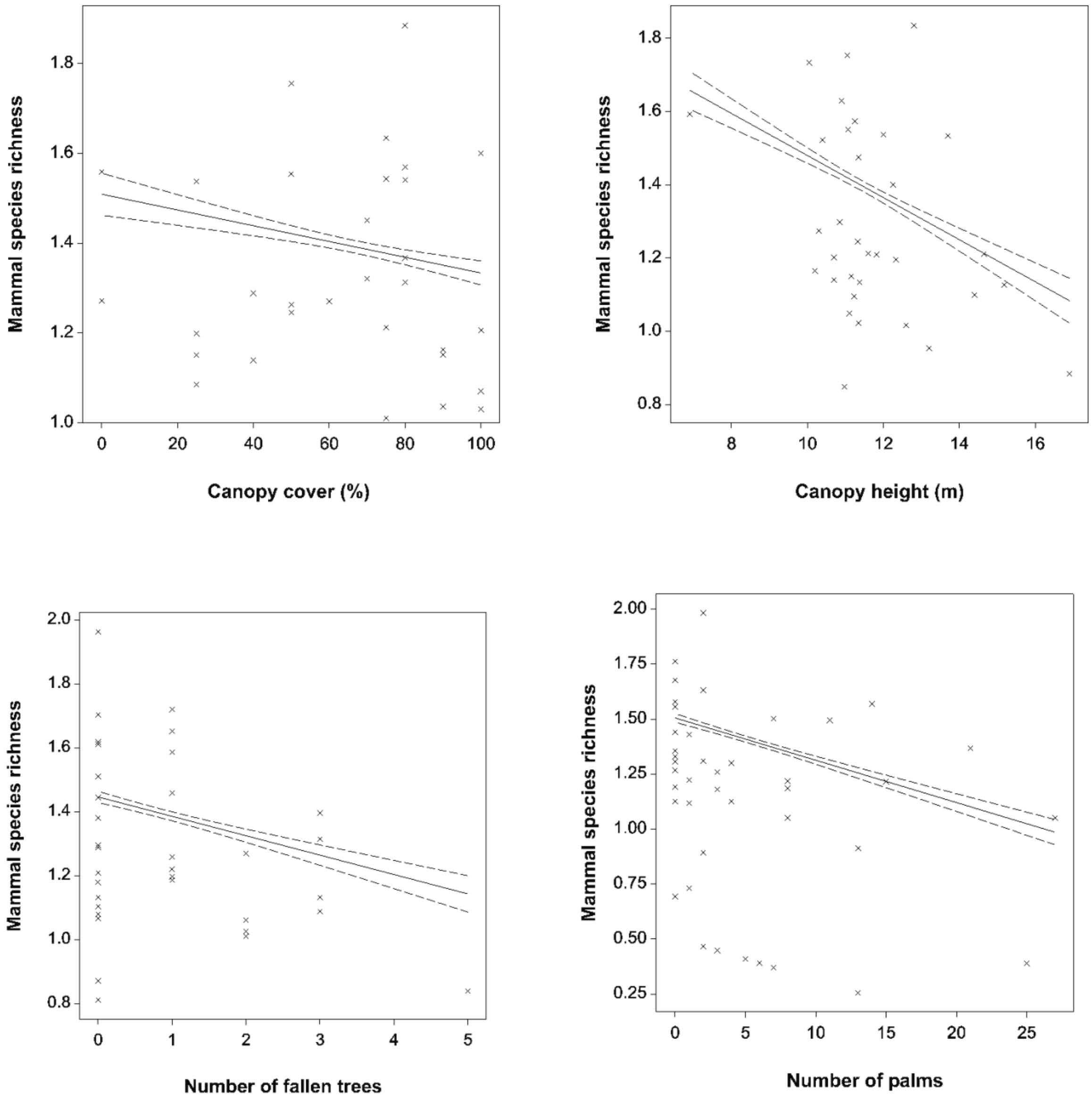
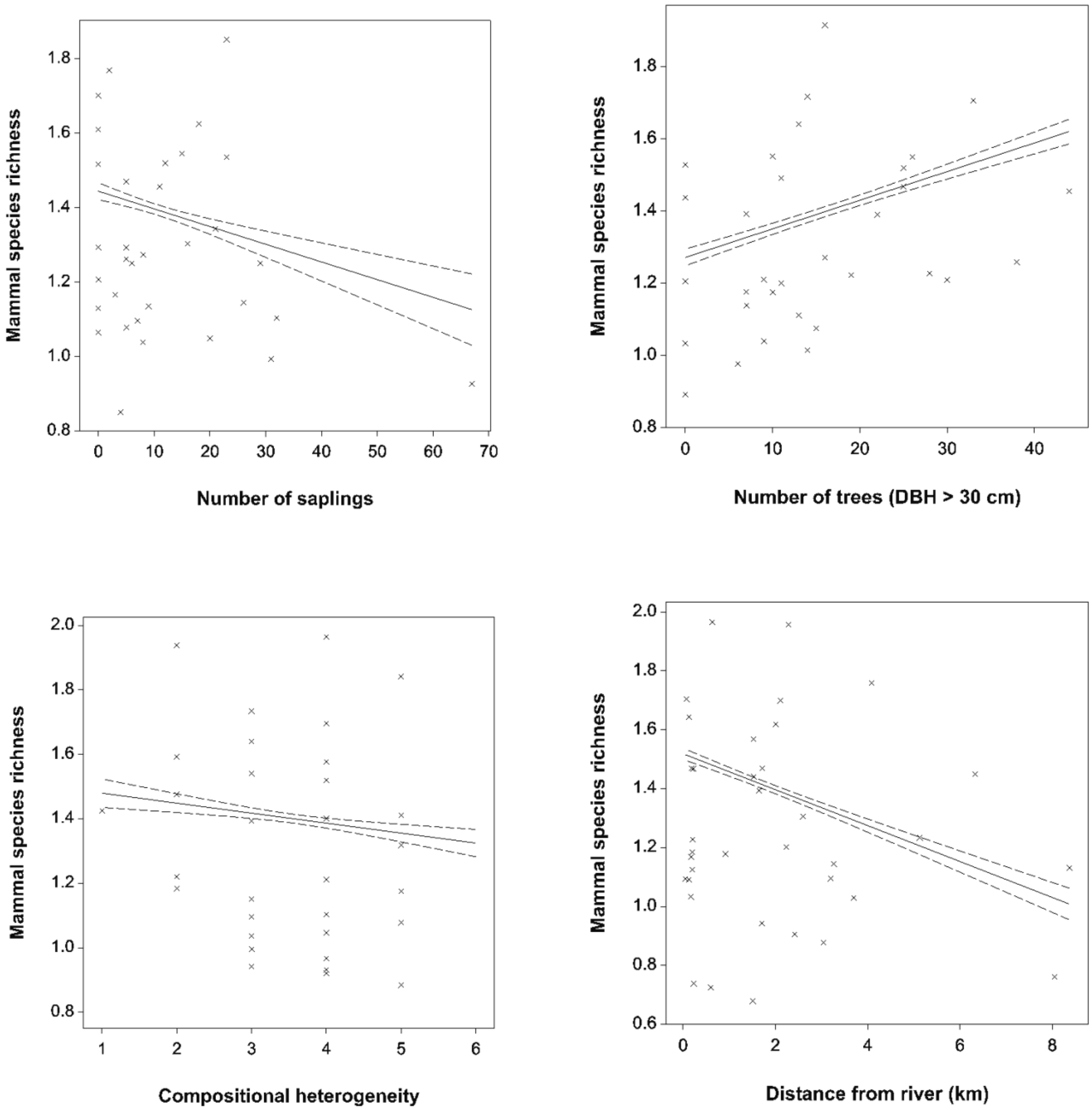


Figure 2. Animal photos captured by trail cameras in the NSPSF. The native mammals include high conservation value species such as Black Panther (top left), Asian Tapir (top right), Malayan Sun Bear (bottom left), and the rare Bearded Pig (bottom right).

Figure 3. Scatter plots showing relationships between mammal species richness and key local- and landscape-level attributes. Scatter plots have 95% confidence intervals (dashed) on the regression (solid) line.




Mammal species richness
Number of saplings
Mammal species richness
Number of trees (DBH > 30 cm)
Mammal species richness
Compositional heterogeneity
Mammal species richness
Distance from river (km)

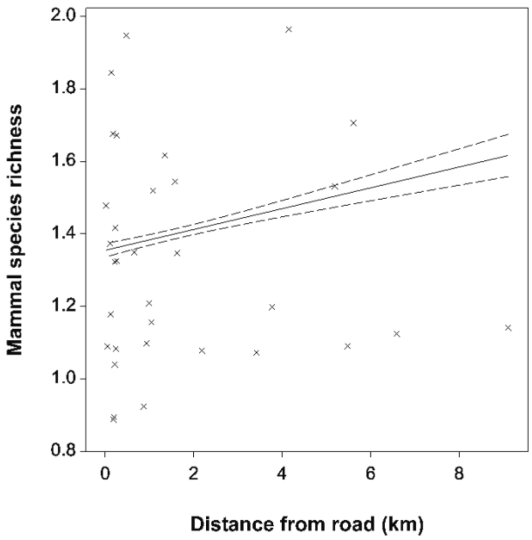

2.0
1.8
1.6
1.4
1.2
1.0
0.8
Mammal species richness
0
2
4
6
8
Distance from road (km)

Table 1. Summary statistics for local-level and landscape-level attributes.

Predictor variable	Mean	Median	Range (max-min)	Standard deviation
Canopy cover (%)	64	75	100	29.21
Canopy height (m)	11.70	11.32	10	1.828
Number of fallen trees with DBH < 45cm	0.911	0	4	1.125
Number of fallen trees with DBH > 45cm	0.0444	0	1	0.208
Number of forest palms	5.133	2	27	6.717
Number of saplings	11.71	8	67	12.59
Number of trees with DBH < 45cm	12.53	41	41	9.922
Number of trees with DBH > 45cm	1.489	1	8	1.984
Landscape compositional heterogeneity	3.756	4	5	1.090
Distance from nearest river (km)	1.770	1.51	8.32	2.021
Distance from nearest road (km)	1.445	0.32	9.09	2.102
Forest area (ha)	257.0	285.8	158.3	52.39
Oil palm area (ha)	42.63	6.02	154.3	49.21

Table 2. Mammal species recorded in camera surveys in the North Selangor Peat Swamp Forest (NSPSF).

Mammals species	**Feeding guild**	**Families**	**IUCN status**	**Number of sites detected**	**Number of images**
Asian Tapir (*Tapirus indicus*)	Herbivore	Tapiridae	Endangered	18	908
Malayan Sun Bear (*Helarctos malayanus*)	Omnivore	Ursidae	Vulnerable	17	391
Bearded Pig (*Sus barbatus*)	Omnivore	Suidae	Vulnerable	6	134
Pig-tailed Macaque (*Macaca nemestrina*)	Omnivore	Cercopithecidae	Vulnerable	11	294
White-thighed Surii (*Presbytis siamensis*)	Herbivore	Cercopithecidae	Near threatened	2	36
Black Panther (*Panthera pardus*)	Carnivore	Felidae	Near threatened	11	374
Large Indian Civet (*Viverra zibetha*)	Carnivore	viverridae	Near threatened	1	3
Lesser Mousedeer (*Tragulus kanchil*)	Herbivore	Tragulidae	Least concern	10	30
Greater Mousedeer (*Tragulus napu*)	Herbivore	Tragulidae	Least concern	2	21
Southern Red Muntjak (Muntiacus muntjak)	Herbivore	Cervidae	Least concern	1	3
Leopard Cat (*Prionailurus bengalensis*)	Carnivore	Felidae	Least concern	1	6
Small Asian Mongoose *(Herpestes javanicus)*	Carnivore	Herpestidae	Least concern	1	6
Wild Boar (*Sus scrofa*)	Omnivore	Suidae	Least concern	34	2761
Long-tailed Macaque (*Macaca fascicularis*)	Omnivore	Cercopithecidae	Least concern	2	9
Malayan Porcupine (*Hystrix brachyura*)	Omnivore	Hystricidae	Least concern	3	15
Common Palm Civet (*Paradoxurus hermaphrodites*)	Omnivore	Viverridae	Least concern	1	6

Table 3. Mammal species richness model were fitted to a dataset and the best nine subsets (out of 44 subsets) with various terms selected based on minimum AIC_C value. The Akaike weight was used as the probability that the selected model is the best model. The top models (i.e. K = 6 for local-level effects and K = 3 for landscape-level effects) have weights more than 0.90. This indicates robust inferences could be made using just those models. The predictor variables are coded as follows: DRV, distance to nearest large river; DRD, distance to nearest road; OP, nearest oil palm plantation; CHG, compositional heterogeneity; CC, canopy cover; CH, canopy height; P, number of palmae species; S, number of saplings; TDBHM30, number of trees more than 30 cm; FTDBHM45, number of fallen trees more than 30 cm.

K: Terms	**R^2**	**AIC_C**	**ΔAIC_C**	**Relative likehoods**	**Akaike weights Wi**
Local-level effects					
1 : P	22.19	1606.19	383.68	0.000	0.000
2 : P+TDBHM30	27.34	1503.49	280.98	0.000	0.000
3 : P+TDBHM30+S	32.71	1396.59	174.08	0.000	0.000
4 : CH+P+TDBHM30+S	37.43	1302.80	80.29	0.000	0.000
5 : CH+P+FTDBHM30+TDBHM30+S	40.36	1245.74	23.23	0.000	0.000
6 : CC+CH+P+FTDBHM30+TDBHL45+S	41.63	1222.51	0.00	1.000	1.000
Landscape-level effects					
1: DR	20.02	1650.4	99.1	0.000	0.000
2: DR+DRD	24.44	1562.6	11.3	0.004	0.004
3: DR+DRD+CHG	25.11	1551.3	0.00	1.000	0.996