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Mammal species composition and habitat associations in a commercial forest and mixed-plantation landscape

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Corresponding Author:	Shyamala Ratnayeke Sunway University MALAYSIA
First Author:	Wai Pak Ng
Order of Authors:	Wai Pak Ng
	Frank T. van Manen
	Stuart P. Sharp
	Siew Te Wong
	Shyamala Ratnayeke
Abstract:	Commercial forest plantations of fast-growing species have been established globally to meet increasing demands for timber, pulpwood, and other wood products. Industrial plantations may contribute to tropical forest conservation by reducing exploitation of primary and secondary natural forests. Whether such plantations can support critical elements of biodiversity, including provision of habitat and movement corridors for species of conservation concern, is an important question in Southeast Asia. Our objectives were to investigate relationships between habitat gradients and community attributes of medium-sized to large mammals in a mixed plantation mosaic in Bengkoka Peninsula, Sabah, East Malaysia. Data on mammals were collected using 59 remote camera stations deployed for a minimum of 21 days (24-hour sampling occasions) in three major land-use types: natural forest, Acacia plantations, and non-Acacia (oil palm, rubber, young Eucalyptus pellita). We used sample-based rarefaction to evaluate variation in species richness with land use and generalized linear models and ordination analyses to evaluate whether variation in mammal detections and species composition were associated with habitat gradients. We recorded >22 mammal species over 1,572 sampling occasions. Natural forest area was positively associated with mammal species richness and detections of threatened mammals. Overall detections of mammals increased with decreasing elevation, but decreased within, and close to, Acacia plantations. Detections of threatened mammals increased with greater proportions of natural forest and Acacia and increasing proximity to roads. Sample-based rarefaction curves indicated that species richness of mammals in Acacia and natural forest was considerably higher than observed. Both natural forest and Acacia plantations shared similar values for species richness and diversity, but non-Acacia plantations scored lower in both metrics. Ordination analyses revealed that mammal species composition differed among different types of land use, with smaller generalists using non-Acacia and a variety of other mammals, including threatened species such as sun bears (Helarctos malayanus) and western tarsiers (Tarsius bancanus), using natural forest, Acacia, or a combination of the two. Our results suggest that Acacia plantations possess attributes supporting a diversity of mammal species, including those we defined as threatened based on IUCN criteria. This may be a function of the habitat mosaic with natural forest in the study area and the mangrove forests on the fringes of the peninsula, which are likely refuges of mammal diversity. Their retention and restoration, therefore, may enhance the conservation potential of industrial Acacia plantations. Additionally, controlled road access in conjunction with anti-poaching operations and strengthening public awareness are essential to reduce the threat of overexploitation.
Suggested Reviewers:	William McShea Smithsonian Institution Conservation and Research Center: Smithsonian's National

	Zoo & Conservation Biology Institute mcsheaw@si.edu This individual has conducted similar work in East Malaysia
	Susan Cheyne s.cheyne@borneonature.org This individual has conducted similar studies in Borneo
	Jedediah Brodie brodie@biodiversity.ubc.ca Relevant expertise
	John Parrotta jparrotta@fs.fed.us

15 Nov, 2020

Editor in Chief
Forest Ecology and Management
Dan Binkley
School of Forestry
Northern Arizona University
Flagstaff, AZ 86011, USA

Submission of manuscript

Dear Professor Binkley,

We are very pleased to submit our manuscript titled 'Mammal species composition and habitat associations in a commercial forest and mixed-plantation landscape' by Wai Pak Ng et al. for your consideration as a publication in *Forest Ecology and Management*.

Conversion of tropical lowland rainforest to agriculture or industrial tree plantations is a major driver of habitat loss for native species in Southeast Asia. This study was conducted in an industrial forest mosaic in Pitas District, Sabah, in Malaysian Borneo, where most natural forest remained as small isolated fragments. We used remote camera data to investigate relationships among habitat and community attributes of mammals in the study area. A key finding from our study was that mammal species richness was comparable to that reported from surveys in protected areas, but that natural forest remnants in the study area may play an important role in the persistence of those species. Another key finding was that a few species, listed as globally threatened, were associated with Acacia plantations. Thus, Acacia plantations possess attributes for supporting a diversity of mammal species, but this potential may depend largely on the location of the site and the retention of a mosaic of native habitat.

This manuscript is our original unpublished work and has not been submitted to any other journal for review. All the authors listed have approved the manuscript and agreed with its submission to *Forest Ecology and Management*. We would greatly appreciate your consideration of our manuscript for review and look forward to your response.

Sincerely,

S. Ratnayeke

Shyamala Ratnayeke
Associate professor
Department of Biological Sciences
Sunway University
No.5, Jalan Universiti, Bandar Sunway,
47500 Selangor Darul Ehsan, Malaysia.

Highlights

- Landscape conditions influence the composition of mammal communities in agroforests.
- Mammal detections and species richness are positively associated with the area of natural forest in the plantation mosaic.
- Mammal detections decrease within and close to the edge of *Acacia mangium* plantations.
- Detections of threatened mammals increase where extents of natural forest and planted *Acacia mangium* are greater, and at sites close to roads.

Title: **Mammal species composition and habitat associations in a commercial forest and mixed-plantation landscape**

Authors: Ng Wai Pak[1], Frank T. van Manen[2], Stuart P. Sharp[3], Siew Te Wong[4], Shyamala Ratnayeke[1]

Affiliations:

[1] *Department of Biological Sciences, Sunway University, Malaysia* ngwaipak@hotmail.com

[2] *U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Bozeman, MT, USA* fvanmanen@usgs.gov

[4] *Lancaster Environment Centre, Lancaster University, UK* s.sharp2@lancaster.ac.uk

[5] *Bornean Sun Bear Conservation Centre, Sabah, Malaysia* wongsiew@hotmail.com

Corresponding author:

Shyamala Ratnayeke, Department of Biological Sciences, Sunway University, Malaysia.

shyamalar@sunway.edu.my

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ABSTRACT

Commercial forest plantations of fast-growing species have been established globally to meet increasing demands for timber, pulpwood, and other wood products. Industrial plantations may contribute to tropical forest conservation by reducing exploitation of primary and secondary natural forests. Whether such plantations can support critical elements of biodiversity, including provision of habitat and movement corridors for species of conservation concern, is an important question in Southeast Asia. Our objectives were to investigate relationships between habitat gradients and community attributes of medium-sized to large mammals in a mixed plantation mosaic in Bengkoka Peninsula, Sabah, East Malaysia. Data on mammals were collected using 59 remote camera stations deployed for a minimum of 21 days (24-hour sampling occasions) in three major land-use types: natural forest, *Acacia* plantations, and non-Acacia (oil palm, rubber, young *Eucalyptus pellita*). We used sample-based rarefaction to evaluate variation in species richness with land use and generalized linear models and ordination analyses to evaluate whether variation in mammal detections and species composition were associated with habitat gradients. We recorded >22 mammal species over 1,572 sampling occasions. Natural forest area was positively associated with mammal species richness and detections of threatened mammals. Overall detections of mammals increased with decreasing elevation, but decreased within, and close to, Acacia plantations. Detections of threatened mammals increased with greater proportions of natural forest and Acacia and increasing proximity to roads. Sample-based rarefaction curves indicated that species richness of mammals in Acacia and natural forest was considerably higher than observed. Both natural forest and Acacia plantations shared similar values for species richness and diversity, but non-Acacia plantations scored lower in both metrics. Ordination analyses revealed that mammal species composition differed among different types of land use, with smaller generalists using non-Acacia and a variety of other mammals, including threatened species such as sun bears (*Helarctos malayanus*) and western tarsiers (*Tarsius bancanus*), using natural forest, Acacia, or a combination of the two. Our results suggest that Acacia plantations possess attributes supporting a diversity of mammal species, including those we defined as threatened based on IUCN criteria. This may be a function of the habitat mosaic with natural forest in

the study area and the mangrove forests on the fringes of the peninsula, which are likely refuges of mammal diversity. Their retention and restoration, therefore, may enhance the conservation potential of industrial *Acacia* plantations. Additionally, controlled road access in conjunction with anti-poaching operations and strengthening public awareness are essential to reduce the threat of overexploitation.

Keywords: fast-growing tree species; mammal species composition; conservation of mammals; Southeast Asia; East Malaysia

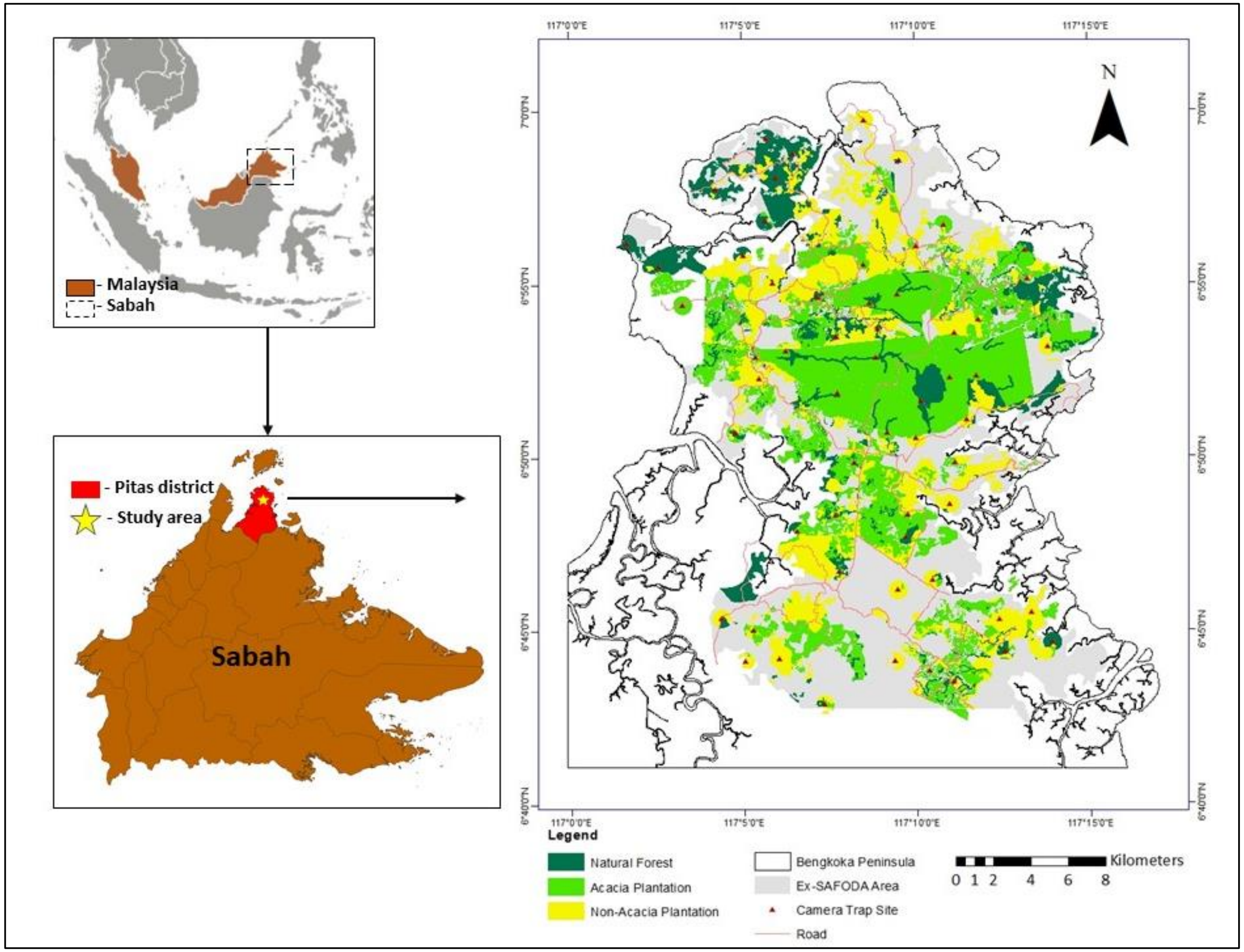
1. INTRODUCTION

In the past few decades, large areas of tropical rainforest have been lost to logging, expanding infrastructure, and conversion to agriculture (Hansen et al. 2013, Giam 2017). The issue is particularly pressing in Southeast Asia, with forest loss fuelled by population growth, economic development, and the global demand for natural resources such as tropical hardwoods, rubber, and palm oil (Laurance, 2007; Sodhi et al., 2009; Wilcove et al., 2013). Between 2000 and 2010, Borneo lost an average of 500,000 ha/year of forest, mostly involving lowland rainforest and peat swamps that are important strongholds of tropical biodiversity (Miettinen et al., 2011). Over 40% of natural forests in Sabah have been lost and few areas sustain primary forests that have not experienced intense logging (McMorrow and Talip, 2001). The direct and indirect effects of total forest loss, agri-conversion, and timber extraction are expected to impact ecosystem services, human social and economic welfare, and forest-dependent species in multiple ways, particularly with respect to food, suitable living space, poaching pressure, and conflict with humans (Meijaard et al., 2005; Dohrenbusch and Bolte, 2007; Butler, 2019).

Sustainable management of tropical forest resources is crucial for maintaining essential ecosystem services and reducing the loss of biodiversity (Sodhi et al., 2010; Struebig et al., 2015). Toward this end, Malaysia has established commercial forest plantations of fast-growing exotic trees such as acacias and eucalypts to meet the growing demand for timber, pulpwood, and other wood products (Gaveau et al., 2016). Commercial forest plantations typically consist of extensive areas of monocultures with reduced biodiversity, but may contribute to tropical forest conservation by reducing further exploitation of primary and secondary natural forests. Additionally, commercial forest plantations could potentially continue to provide important ecosystem services by serving as watersheds, reducing soil erosion, and sequestering atmospheric carbon (Dohrenbusch and Bolte, 2007; Krisnawati et al., 2011; Braakhekke et al., 2019; Nath et al., 2019). An important question is whether such plantations can support critical elements of biodiversity, including habitat and movement corridors for species of conservation concern. This propensity may be realized only if substantial patches of natural forest are retained (Edwards et al., 2012), but further research is urgently needed.

The capacity of selectively logged forests or monoculture forest plantations to support vertebrate species, including large to medium-sized mammals, is a pressing conservation issue (Norris et al., 2008; Brodie et al., 2015). Mammals are particularly vulnerable to habitat loss and overexploitation and have consequently received much conservation attention (Wilcove et al., 2013). A quarter of all mammal species are threatened with extinction (The International Union for Conservation of Nature [IUCN], 2019), with current extinction rates well above background rates (Barnosky et al., 2011). Mammals in the Indomalayan region are particularly at risk (Sodhi et al. 2009; Hoffman et al., 2011). In Southeast Asia, threats from habitat loss and poaching are decimating mammal populations (Sodhi et al., 2010), with some studies predicting that 21–48% of mammals in this region may be extinct by 2100 (Brook et al., 2003). These threats are compounded by ecological traits such as large area requirements, special resource requirements, migratory habits, and low population densities (Western et al., 2009). Several species of mammal play keystone roles in ecosystems by dispersing seeds, maintaining the composition of plant communities through grazing (Young et al., 2013), or maintaining biodiversity through the cascading effects of predation (Terborgh et al., 2001). Large charismatic mammals are important conservation flagships and conservation umbrellas through their sensitivity to human disturbance, co-occurrence with other species of conservation concern and large area requirements (Noss, 1990; Caro, 2003; Ratnayeke and van Manen, 2012; Brodie et al., 2015). Moreover, variation in the type and intensity of habitat alteration can influence mammalian assemblages, which thus have the potential to serve as useful indicators of habitat disturbance (Cheyne et al., 2016).

Borneo is among the 18 regions of the world supporting megadiversity, including 288 species of terrestrial mammal (Budiharta and Meijaard, 2017). Approximately 40% of Borneo’s mammal species are classified under various level of conservation risk (IUCN, 2019). Between 1973 and 2010, Borneo’s forest cover (558,060 km^2) declined by 30%, with 10% (75,480 km^2) of forests replaced by industrial oil palm and commercial timber plantations; the highest forest loss was in the Malaysian state of Sabah (Gaveau et al., 2014). Wildlife inventories report the persistence of large Bornean mammals in degraded forest or in portions of timber and oil palm plantations adjoining natural forests. These typically include bearded pig, *Sus barbatus*, sambar deer, *Rusa unicolor*, Bornean yellow muntjac, *Muntiacus atherodes*, sun bears, *Helarctos malayanus*, (McShea et al., 2009; Guharajan et al. 2018), and the Critically Endangered Bornean orangutan (*Pongo pygmaeus*; Meijaard et al., 2010). A major goal of sustainable forestry is to develop integrated land-use systems that preserve valuable elements of biodiversity and ecosystem processes (Bruenig, 1996). Industrial forests need not necessarily be at odds with wildlife conservation if they can be managed in a manner that enhances and maintains wildlife populations and may serve as temporary refuges and important wildlife corridors between fragments of more suitable habitat. Research aimed at identifying factors associated with the distribution and diversity of mammals within industrial forest mosaics will contribute to this purpose. The goal of our study was to determine the associations between species assemblages of mammals and habitat characteristics of a commercial forest mosaic in Sabah, East Malaysia.


- Malaysia
- Sabah
- Pitas district
- Study area
Sabah
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6°45'0"N
6°40'0"N
Legend
Natural Forest
Acacia Plantation
Non-Acacia Plantation
Bengkoka Peninsula
Ex-SAFODA Area
Camera Trap Site
Road
Kilometers
0 1 2 4 6 8

Figure 1: Study area showing land use in Bengkoka Peninsula, District of Pitas, Sabah, Malaysia. Ex-SAFODA (former Sabah Forestry Development Authority) areas were a mix of *Acacia mangium*, hill rice, burned or fallow land, and oil palm and rubber plantations.

2.0 METHODOLOGY

2.1 *Study area*

The study area was located in Bengkoka Peninsula (6^0 49' 55" N and 117^0 09' 32" E; Figure 1), which is situated at the northern tip of Sabah, on the island of Borneo, Malaysia. Lowland dipterocarp forest and coastal mangrove once covered the area. In 1983, a 60-year concession was granted to the Sabah Forestry Development Authority (SAFODA) to log and plant an area of approximately 25,000 ha in the peninsula with *Acacia mangium* (Kwiheng Wood and Environmental Consultants [KWEC] 2009). Since the gazetting, an intensive program of planting, maintenance, and harvest was established. More than half the area consisted of *Acacia mangium* (Table 1) managed by two plantation companies, Acacia Forest Industries Sendirian Berhad (AFISB) and Gerak Saga Sendirian Berhad (GSSB). Plantation compartments were established from a combination of Acacia plantation and natural regeneration after wildfires (Acacia wildings). Weeding, fertilizing, and thinning were the most common forms of silvicultural management in the first two years after saplings were planted. Harvesting for paper pulp was carried out on stands that were 7–8 years old. Older stands of 10–12 years were harvested for timber.

Since 2014, *Eucalyptus pellita* has been used to gradually replace *Acacia mangium* in harvested compartments. Patches of privately-owned oil palm and rubber plantation were also found in the study area and together with new stands of *Eucalyptus pellita*, were classified under the land-use type non-*Acacia* (Table 1). Ex-SAFODA land areas were given back to local communities (Figure 1). We sampled these areas as well.

About 18% of the study area consisted of native vegetation that was retained for the conservation of wildlife and water resources. This included mangroves, wetlands, and selectively logged secondary forest, water catchments, river buffers, and a few small patches of fallow land (AFISB, 2016). These were classified as natural forest (Table 1). Areas of coastal mangrove that were under the jurisdiction of the Sabah Forestry Department were excluded from our study.

There were 63 villages, 10 primary schools, and 2 secondary schools in the peninsula. Livelihoods of local indigenous people were derived primarily from hill paddy farming, working in the commercial timber plantations, hunting, and fishing (AFISB, 2016).

Table 1: Percentage of three different land-use types within Acacia Forest Industries and Gerak Saga areas, Bengkoka Peninsula, Sabah, Malaysia, 2016–2017.

Land-use type	AFI area (ha)	GS area (ha)	Total Land (ha)	%
Natural forest[a]	3,741	693	4,434	17.5
Acacia plantation	7,415	5,758	13,173	52.0
Non-*Acacia* plantation[b]	7,711	0	7,711	30.5
Total	18,867	6,451	25,318	100.0

[a] Mangrove, wetlands, logged-over forest, water catchment, river buffers, or fallow land.
[b] Planted with *Hevea brasiliensis*, *Elaeis guineensis*, or *Eucalyptus pellita*.

2.2 *Remote camera survey*

We deployed remote cameras (Moultrie M990i Gen2, Pradco Outdoor Brands, Alabama) during the inter-monsoon season between 10 April and 7 December 2017. We used ArcMap 10.3.1 (Esri, Redlands, California, USA) to randomly select camera sites across the three different land-use types: natural forest, *Acacia* plantation, and non-*Acacia* plantation, to capture a gradient of habitat conditions. We maintained a minimum spacing of 1 km among camera sites (Wemmer et al. (2004), to enhance independence between them. Cameras were positioned at 40–50 cm above ground (Giman et al., 2007) and 10 g of scent lure (shrimp paste, locally sourced) was hung ~1 m above ground level and 2.5 m in front of the camera to improve detection. The lure had been shown previously to be effective at attracting a wide range of mammals during trials in Bengkoka Peninsula and at Tabin Wildlife Reserve, Sabah. We set cameras to collect data for 21 consecutive sampling occasions of 24 hours, programmed with a 1-min delay between photographs with each event accompanied by a 10-sec video. We checked cameras weekly to replace memory cards, batteries, and bait. We developed this sampling design to enhance detection of mammal species occurring within a 500-m radius of the camera (Holinda et al. 2020).

2.3 *Environmental variables for model fitting*

We obtained data for 10 natural and anthropogenic environmental covariates from GIS databases maintained by AFISB and GSSB. For each camera site, we measured the distance (m) to the nearest edge of specific land-use types using ArcMap 10.3.1 Spatial Analyst Tools (Esri, Redlands, California, USA). For area (ha) measurements, we calculated a 500-m buffer around each camera site, which we considered sufficient to reflect habitat covariates potentially selected by mammals detected by the camera. Covariates measured at each sampling site included: 1) elevation, 2) distance to nearest human settlement, 3) distance to nearest road, 4) distance to nearest river, 5) area of natural forest (i.e., river buffer, forest reserve, mangrove or associated mangrove, secondary/regenerated forest), 6) area of *Acacia* plantation, and 7) area of non-*Acacia* plantation (*Hevea brasiliensis*, *Elaeis guineensis*, *Eucalyptus pellita*). We included 3 binary covariates: distances <1000 m or >1000 m from the edge of natural forest, *Acacia* plantation, and non-*Acacia* plantation. We created raster layers for all these covariates with a spatial resolution of 130 m.

2.4 *Data analysis*

We deployed 24 camera sites in natural forest, 24 in *Acacia* plantations, and 11 in non-*Acacia* plantations. Cameras were operated for a total of 1,572 sampling occasions of 24 hours, with 621, 647, and 304 occasions, respectively, in *Acacia*, natural forest, and non-*Acacia*. We used the remote camera images and videos to identify mammals to species level based on Phillipps and Phillipps (2016), IUCN (2019), and confirmation by experts. When image clarity image or small body size hindered identification at the species level, we grouped images within a common genus, family, or order. These included rodents, civets, muntjac, mouse deer, and otters. Images of tree shrews (Order Scandentia), were usually indistinguishable from squirrels (Order Rodentia, Family Sciuridae) and were grouped together. Species grouped together were counted as a single species when measuring species richness.

We calculated camera detection rates (D) as the number of independent photographs of a species detected (C) per 100 sampling occasions using the formula: $D = C \times 100 / \sum N$, where $\sum N$ was the total number of sampling occasions accumulated over the study (Bernard et al., 2014). Because multiple photos of a species within the same day may not represent independent detections (Royle et al., 2009), we considered the detection of a species at a camera site within a 24-hour period as an independent detection.

Observed values of species richness are influenced by sampling effort (i.e., number of sampling occasions and number of camera stations). Biodiversity samples are usually incomplete, and some species, although present are not detected (Chao et al., 2014). Because area and sampling intensity differed among land-use types, we compared sampling effort (sample completeness) by constructing sample-based rarefaction and extrapolation (*R*/*E*) curves (Chao and Jost, 2012) to estimate the 'true' or effective number of species (i.e., estimated species richness; Colwell et al., 2012). We standardized data for camera sites to 21 sampling occasions and tabulated presence and absence for each species recorded. We used these data to estimate Shannon and Simpson diversity indices, which account for the evenness or skewness of species observations. Curves were based on incidence data, with 95% confidence intervals based on 5,000 bootstrap replicates, and generated using the iNEXT package (Hsieh et al., 2016) in the R environment 3.5.3 (R Core Team 2019).

We used Poisson regression to investigate relationships between mammal count data (species richness, total mammal detections, total threatened mammal detections) as response variables and the 10 environmental covariates as predictor variables. Poisson regression is particularly suited for count data that tend to have skewed frequency distributions (Jones et al., 2002). We defined threatened mammals as those listed by the IUCN as Critically Endangered, Endangered, or Vulnerable (IUCN, 2019). We standardized covariates to a mean of 0 and a standard deviation of 1 (Ramette, 2007).

We used an information-theoretic approach to assess model fit among a set of *a priori* models. Generation of the model set was preceded by investigating individual covariates visually and selecting those that showed a potential relationship with the response variable (Anderson, 2007; Grueber et al., 2011). We then generated Poisson models to examine the association between the response variable and plausible combinations of predictor variables (Warton et al., 2016). Because the total number of sample sites was 59, we limited the number of covariates in any single model to four or fewer.

Poisson regression relies on the assumption that the variance and mean of the response variables are similar. We used a regression-based *t*-test (Cameron and Trivedi, 1990) of this assumption in package AER (Kleiber and Zeileis, 2008). Where overdispersion was evident, we used negative binomial models in lieu of Poisson models. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c; Akaike, 1974) to rank and select the most plausible models (Burnham and Anderson, 2002). If no single best model was evident, we calculated a weighted average of parameter estimates of models within 2 AIC_c units of the highest-ranked model (Grueber et al., 2011) using package MuMln (Barton, 2019). We used package faraway (Faraway, 2016) to check for multicollinearity among variables using the Variance Inflation Factor (VIF).

We generated prediction maps for species richness and mammal detections by applying the regression equations to each 130-m pixel. We limited spatial inference to pixels contained within the study area, that is, areas for which land use data were available. We used Spatial Analyst tools in ArcGIS (ESRI, Redlands, CA, USA; v.10.6) to calculate predictions separately for each of the models with $\Delta AIC_c \leq$ 2.0. For the binary covariates we created a map layer with pixel values of 1 for areas within 1000 m of *Acacia* and values of 0 for >1000 and multiplied the layer with the respective coefficient. We then multiplied each layer with their respective AIC_c weights and summed these layers to create a final map depicting the model-averaged predictions for species richness and number of mammal detections.

We used canonical correspondence analysis (CCA) to display and evaluate the influence of environmental gradients on variation in mammal species composition. This analysis is based on a unimodal model and represents mammal species responses to environmental variation in an ordination diagram in a reduced spatial dimension (biplot), where sites without species detections are excluded (Ter Braak, 1986). We limited environmental variables to six covariates showing the strongest association with species richness and species detections in regression analyses: 1) elevation, 2) distance to the nearest road, 3) distance to the nearest settlement, and area of 4) natural forest, 5) *Acacia*, and 6) non-*Acacia*. Canonical correspondence analysis is sensitive to rare species, so we used a Chord transformation to reduce the effects of zero-inflated records in the dataset (Ramette, 2007; Borcard et al., 2011). We scaled all covariates as described previously. We conducted a permutational multivariate analysis of variance (PERMANOVA) test of the final model to evaluate the overall influence of environmental covariates on species composition. Analyses were performed using Package vegan (Oksanen, 2018) in the R environment 3.5.3 (R Core Team 2019).

3.0 RESULTS

3.1 *Mammal diversity and land-use types*

Cameras captured 931 total images of native mammal species (Table 2). Individuals that could not be identified to species were grouped within genus or family (i.e., otter [*n* = 4 records], civet [*n* = 124], mousedeer [*n* = 133], muntjac [*n* = 10], rat [*n* = 52]), which resulted in a minimum of 22 species or species groups for analysis (Table 2). Including species documented outside of the sampling period, a total of 34 species or species groups occurred in the study area.

Photographic capture rates were greatest for squirrels/tree shrews, mouse deer, civets, and bearded pigs. Two species were listed as Near Threatened, six species as Vulnerable, one was Endangered (proboscis monkey [*Nasalis larvatus*]), and one was Critically Endangered (Sunda pangolin [*Manis javanica*]) (IUCN 2019). Four species were endemic to Borneo: the proboscis monkey, Malay badger (*Mydaus javanensis*), Bornean porcupine (*Hystrix crassispinis*), and western tarsier (*Tarsius bancanus*).

Table 2: Mammal species detected at 59 remote camera sites in three different land-use types at Bengkoka Peninsula, Sabah, Malaysia, 2016–2017.

Scientific name	Common name	Capture rate per 100 sampling occasions: Natural forest	*Acacia*	Non-*Acacia*	Total	No. sites	IUCN[a]	Diet[b]	Body mass (kg)
Manis javanica	Sunda pangolin	0.2	0.2	0.0	0.1	2	CR	I	2.5–7.0
Nasalis larvatus	Proboscis monkey	0.2	0.0	0.0	0.1	1	EN	H	12.0–24.0
Sus barbatus	Bearded pig	5.1	7.6	2.0	5.5	30	VU	O	45.0–200.0
	Otter spp.	0.3	0.2	0.3	0.3	3	VU	C	2.5–11.0
Macaca nemestrina	Pig-tailed macaque	4.5	3.5	0.7	3.4	19	VU	O	4.0–9.0
Rusa unicolor	Sambar deer	1.1	0.8	0.3	0.8	11	VU	H	200.0
Helarctos malayanus	Sun bear	0.6	0.5	0.3	0.5	7	VU	O	20.0–65.0
Tarsius bancanus	Western tarsier	0.6	2.1	0.0	1.1	6	VU	C	0.2
Ratufa affinis	Pale giant squirrel	0.2	0.2	0.0	0.1	2	NT	H	1.2
Trachypithecus cristatus	Silvered langur	0.2	0.0	0.0	0.1	1	NT	H	4.0–6.5
Hystrix crassispinis	Bornean porcupine	0.0	0.2	0.3	0.1	2	LC	O	2
	Civet spp.	3.4	12.9	7.2	7.9	38	LC	O	2.3–4.7

Prionailurus bengalensis	Leopard cat	0.3	1.1	1.6	0.9	11	LC	C	2.5
Macaca fascicularis	Long-tailed macaque	7.6	2.6	3.6	4.8	27	LC	O	3.0–7.0
Trichys fasciculata	Long-tailed porcupine	0.2	0.0	0.0	0.1	1	LC	O	2
Mydaus javanensis	Malay badger	0.5	0.2	1.6	0.6	6	LC	O	2.5
Echinosorex gymnura	Moonrat	0.2	0.2	0.7	0.3	3	LC	O	1
	Mousedeer spp.	15.8	2.9	4.3	8.5	24	LC	H	2.3–4.3
	Muntjac spp.	0.2	1.3	0.3	0.6	9	LC	H	20.0–28.0
	Squirrel/ treeshrew	28.6	11.3	17.8	19.7	47	LC	-	0.1–0.2
Martes flavigula	Yellow-throated marten	0.6	1.0	0.0	0.6	9	LC	O	1.4
	Rat spp.	5.7	1.0	3.0	3.3	18	-	-	-
	Sum	**75.7**	**49.4**	**44.1**	**59.2**				

[a] IUCN status (IUCN 2019): CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concerned.

[b] Diet guild: I = insectivore; H = herbivore; O = omnivore; C = carnivore.

All land-use types had high to moderately high sampling coverage (86–93%), with non-*Acacia* receiving the lowest sampling coverage because of the relatively small sampling area (Figure 2). Estimated species richness based on extrapolation was similar for *Acacia* and natural forest, but about 35% lower in non-*Acacia* plantations. However, confidence intervals overlapped broadly among all three types of land-use and, except for non-*Acacia* plantations, curves did not reach an asymptote (Figure 2). Thus, estimates of the effective number of species (Table 3; Chao et al., 2014) were considerably higher than those based on extrapolation where sampling intensity was increased to approximately twice the largest reference sample size (i.e., n = 24 or the largest number of camera sites in a habitat type; Figure 2). Simulations indicated that sampling intensity would have to increase nearly 17-fold (i.e., ~400 camera sites) to reach the estimated number of 51 species in natural forest. Both natural forest and *Acacia* plantations shared similar values for Shannon diversity and Simpson diversity (Table 3), but non-*Acacia* plantations scored lower in all measures of diversity. The modest differences between observed and estimated indices for all land-use types suggest that a few abundant species characterized the mammal community and remaining species were rare.

Table 3: Effective diversity measures (asymptotic estimates) for three different types of land use in Bengkoka Peninsula, Sabah, Malaysia, 2016–2017.

	Natural forest		*Acacia*		**Non-***Acacia*	
	Observed	**Estimated**	**Observed**	**Estimated**	**Observed**	**Estimated**
Species richness	20.0	50.7	19.0	39.1	13.0	18.7
Shannon diversity	12.3	14.4	12.0	14.0	10.3	13.2
Simpson diversity	9.8	10.2	9.1	9.5	8.4	9.9

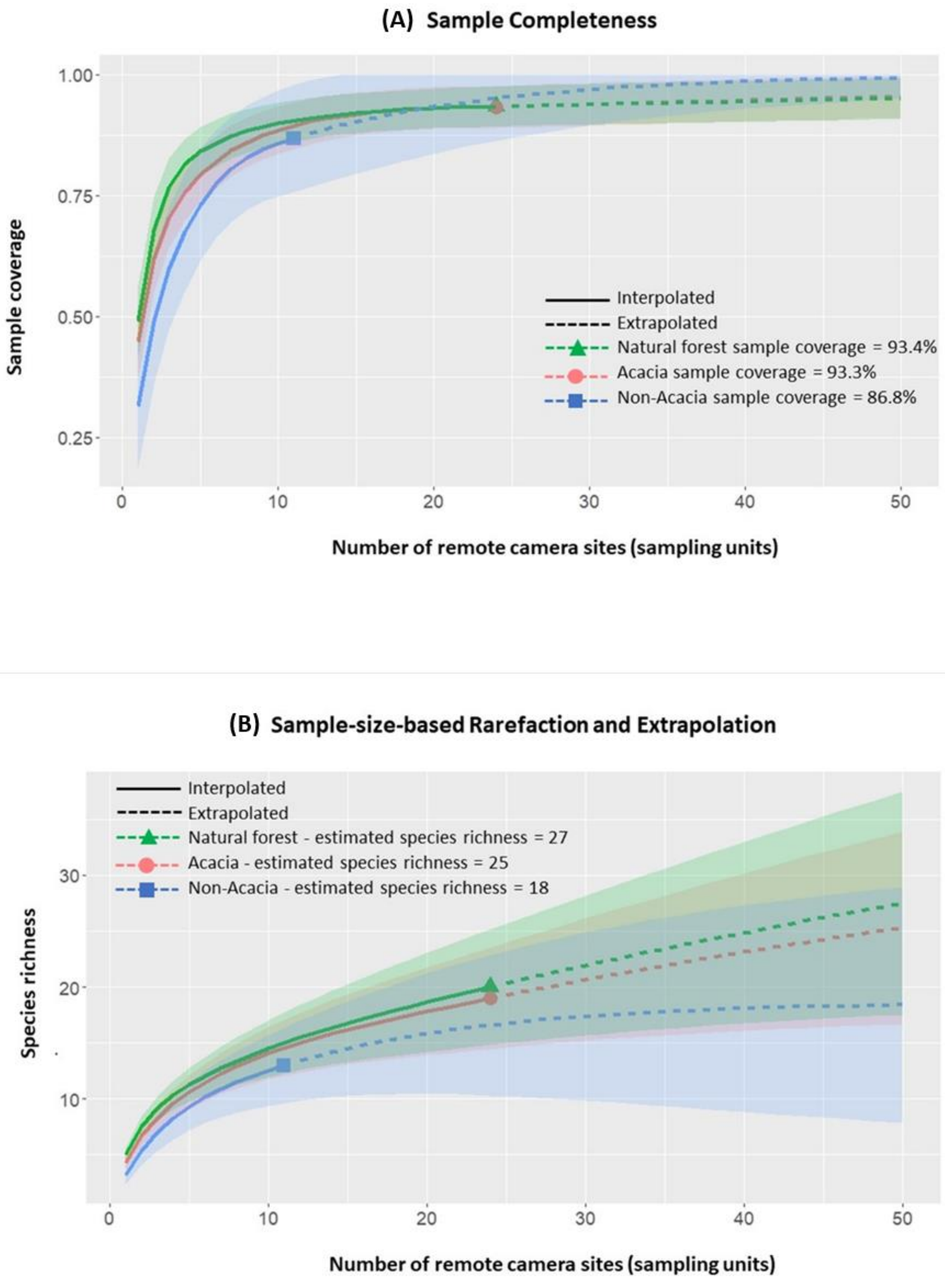

Figure 2: (A) Sample completeness for rarefied samples (solid line) and extrapolated samples (dashed line) and (B) sample-based rarefaction and extrapolation curves of species richness for three major land-use types as a function of sample size, Bengkoka Peninsula, Sabah, Malaysia, 2016–2017. Reference samples are represented by solid icons. Shaded areas represent confidence intervals (95%) based on

5,000 bootstrap replicates. Sampling effort for all land-use types exceeded 85%. Curves were extrapolated to approximately twice the largest reference sample size of 24 obtained for the *Acacia* land-use type.

3.2 *Mammal species richness and detections and environmental gradients*

Poisson models of species richness were not over- or under-dispersed. Also, variance-inflation values were <10 for all covariates indicating little evidence of strong collinearity. The highest-ranking Poisson regression models included area of natural forest and elevation as covariates (Table 4). Model-averaged parameter estimates indicated that the area of natural forest within a 500-m buffer (78.5 ha) of a sample site was the best (although weak) predictor of mammal species richness (Table 5, Figure 3A) with a mean species richness of 4.43 (sd = 0.034) across the entire study area. Based on our sampling sites, which had a mean area of natural forest of 18.1 ha and mean elevation of 35 m, increasing natural forest by 25% would change predicted species richness from 4.62 (the mean species richness at sampling sites) to 4.74, whereas a 25% decline in natural forest would result in a species richness of 4.51. Thus, our models predict that increases/decreases in area of natural forest may have only a modest (2.4% increase) positive effect on species richness.

Poisson models of total mammal detections and threatened mammal detections were over-dispersed, so we used the negative binomial distribution. Covariates predicting variation in total mammal detections appeared in four models with $\Delta AIC_c \leq 2$ (Table 4, Supplementary Figure 1). Mammal detections were greater at distances >1000 m from the nearest edge of *Acacia* plantations and with decreasing elevation (Table 5, Figure 3B). On average, 17.9 mammal detections occurred across all camera sites, dropping to 14.3 detections at sites inside *Acacia* plantations or within 1000m from their periphery, and increasing to 22.4 at sites >1000m from the periphery of *Acacia*.

Two negative binomial models captured 69% of the total AIC_c weight of habitat models for threatened species, averaging 3.4 detections of threatened species per site (Table 4, Supplementary Figure 2). Detections of threatened mammals increased where the area of natural forest and *Acacia* plantations were greater, and in close proximity to roads (Table 5). Based on our sampling sites, which had a mean area of *Acacia* of 25.4 ha, increasing the area of *Acacia* or natural forest by 25% would increase threatened species detections to 4.15 and 4.1 respectively.

Table 4: Generalized linear regression results of the top 10 *a priori* models to assess habitat variables associated with mammal species richness (Poisson models), all mammal detections (negative binomial models), and threatened mammal detections (negative binomial models) at Bengkoka Peninsula, Sabah, Malaysia, 2016–2017. A detection was one or more mammal species documented at a remote camera site during a sampling occasion of 24 hr.

Dependent variable	**Model**[a]	**AIC_c**[b]	**ΔAIC_c**[c]	**ML**[d]	**w_i**[e]	**Df**[f]
Mammal species richness	nat.for	230.5	0.00	1.00	0.19	2
	null model	231.9	1.40	0.50	0.10	1
	elevation + nat.for	232.3	1.85	0.40	0.08	3
	d.road + nat.for	232.7	2.21	0.33	0.06	3
	nat.for	233.2	2.71	0.26	0.05	2
	elevation	233.4	2.95	0.23	0.04	2
	non-Acacia	233.5	3.01	0.22	0.04	2
	d.road	233.7	3.17	0.21	0.04	2
	Acacia	233.7	3.20	0.20	0.04	2
	elevation + d.nat.for	234.5	4.04	0.13	0.03	3
Total mammal detections	elevation + d.Acacia	414.7	0.00	1.00	0.15	4
	elevation	415.1	0.45	0.80	0.12	3
	elevation + Acacia	415.8	1.09	0.58	0.09	4
	elevation + nat.for	416.2	1.56	0.46	0.07	4
	elevation + d.nat.for	416.7	2.02	0.36	0.06	4
	elevation + d.road + d.Acacia	416.7	2.06	0.36	0.06	5
	elevation + d.road	417.0	2.30	0.32	0.05	4
	elevation + d.road + nat.for	417.5	2.87	0.24	0.04	5
	Acacia	417.7	3.05	0.22	0.03	3
	d.Acacia	417.8	3.16	0.21	0.03	3

Threatened mammal detections	d.road + nat.for + Acacia	252.3	0.00	1.00	0.44	5
	d.road + nat.for + Acacia+ non-Acacia	253.5	1.15	0.56	0.25	6
	d.road + nat.for + Acacia + d.nonAcacia	254.7	2.43	0.30	0.13	6
	nat.for +Acacia	257.3	4.99	0.08	0.04	4
	d.road + nat.for + non-Acacia	258.0	5.71	0.06	0.03	5
	d.road + non-Acacia	258.2	5.89	0.05	0.02	4
	nat.for + Acacia + non-Acacia	259.0	6.70	0.04	0.02	5
	nat.for + Acacia + d.non-Acacia	259.5	7.18	0.03	0.01	5
	d.settle + nat.for + Acacia	259.7	7.40	0.03	0.01	5
	non-Acacia	260.1	7.78	0.02	0.01	3

[a]Habitat variables were area (ha) of natural forest, *Acacia* plantation or non-*Acacia* plantation within a 500-m buffer (i.e., nat.for, Acacia, non-Acacia), elevation, distance to nearest settlement (d.settle), distance to nearest road (d.road), and distance to nearest edge of natural forest, *Acacia* or non-*Acacia* (d.nat.for, d.Acacia, d.non-Acacia).

[b] AIC_c = Akaike's information criterion adjusted for small *n*.

[c] ΔAIC_c = difference in AICc compared with the lowest AIC_c model.

[d] ML = model likelihood.

[e] $\boldsymbol{w_i}$ = AIC_c model weight.

[f] df = number of parameters.

Table 5: Standardized parameter estimates of model-averaged regression models showing the relative influence of different habitat covariates on mammal species richness (Poisson models), all mammal detections (negative binomial models), and threatened mammal detections (negative binomial models) at Bengkoka Peninsula, Sabah, Malaysia, 2016–2017.

Dependent variable	**Parameter**[a]	**Parameter estimate**[b]	**Standard error**	**CI 7.5%**[c]	**CI 92.5%** [c]
Mammal species richness	intercept	1.558	0.061	1.469	1.647
	nat.for	0.110	0.058	0.026	0.194
	elevation	-0.039	0.063	-0.131	0.054
Total mammal detections	intercept	2.832	0.185	2.564	3.100
	elevation	-0.230	0.092	-0.364	-0.096
	d.Acacia	-0.346	0.212	-0.656	-0.037
	Acacia	-0.123	0.094	-0.261	0.014
	nat.for	0.093	0.085	-0.031	0.217
Threatened mammal detections	intercept	0.952	0.130	0.762	1.141
	d.road	-0.426	0.145	-0.638	-0.214
	Acacia	0.698	0.301	0.260	1.135
	nat.for	0.775	0.277	0.372	1.178
	non-Acacia	0.417	0.375	-0.130	0.965

[a]Habitat covariates that appeared in top models included area (ha) of natural forest, *Acacia* plantation or non-*Acacia* plantation within a 500-m buffer (i.e., nat.for, Acacia, non-Acacia), elevation, distance to nearest road (d.road), and distance to nearest edge of *Acacia* plantation (d.Acacia).

[b]Model coefficients based on standardized covariates values to allow comparison of relative importance.

[c]We used 85% confidence intervals following Arnold (2010).

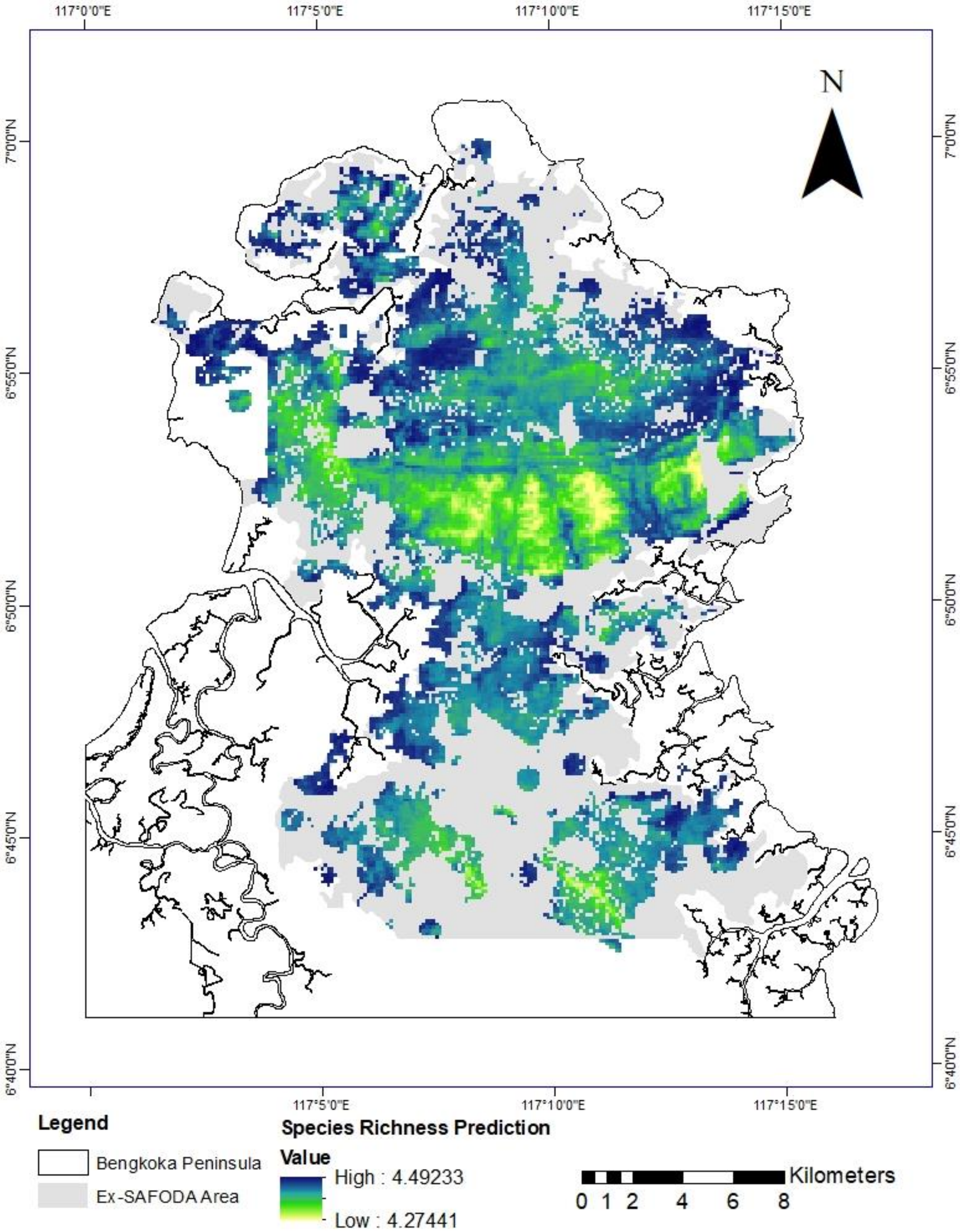

Figure 3. Predictions of species richness based on averaged parameter estimates of regression models, Bengkoka Peninsula, Sabah, Malaysia, 2016–2017. Predictions have been applied only to parts of the study area for which land use data were available.

3.3 *Patterns of mammal species composition among different land-use types*

Environmental covariates contributed significantly to patterns of species distributions, with eigenvalues of 0.2185 and 0.1158 explaining 45% and 24% of the variance of the data for the first 2 canonical axes, respectively. The two axes together explained 69% of the variation in species-environment relationships (Table 6). The overall solution of axes in the CCA ordination was statistically significant (Monte Carlo permutation test with 999 permutations under the reduced model, df = 6, χ^2 = 0.483, F = 1.473, P = 0.006).

Table 6: Summary of canonical correspondence analysis (CCA) results and biplot scores for constraining variables of the first two CCA axes of environmental covariates and mammal species compositions, at Bengkoka Peninsula, Sabah, Malaysia, 2016–2017.

	Canonical axes	
	1	**2**
Eigenvalue	0.2185	0.1158
% of variance explained	45.26	23.99
Cumulative percentage of variance explained	45.26	69.25
Environmental variable		
Elevation	0.6779	0.3892
Distance to settlement	0.0944	0.0014
Distance to road	0.0883	-0.3682
Natural forest area	0.1809	-0.8600
Acacia plantation area	0.7603	0.3287
Non-*Acacia* plantation area	-0.7770	0.3991

A permutation test of the first ordination axis was significant (df = 1, χ^2 = 0.218, F = 3.999, P = 0.004). The top three parameters for axis 1, in order of decreasing influence, were the area of *Acacia* and non-

Acacia plantations, and elevation; the area of natural forest explained most of the variation for the second axis, followed by elevation (Table 6).

Permutation tests revealed three significant environmental factors: elevation (df = 1, χ^2 = 0.128, F = 2.335, P = 0.006), the area of *Acacia* (df = 1, χ^2 = 0.117, F = 2.14, P = 0.007), and the area of natural forest (df = 1, χ^2 = 0.097, F = 1.770, P = 0.048). Biplot relationships showed that elevation, and areas of natural forest, non-*Acacia*, and *Acacia* were the most important parameters shaping the overall mammalian community (Figure 4). Four species (Bornean badger, giant squirrel, otters, and leopard cat) and many small mammals (squirrels and tree shrews) used non-*Acacia* plantations. Detections of otters were few (n = 4) and occurred in all three land-use types (Table 2); its position close to non-*Acacia* in the biplot may be a function of the large percentage of non-*Acacia* at the site where one of the otters was detected. The muntjac, sun bear, sambar deer, bearded pig, Sunda pangolin, and pig-tailed macaque, were associated with *Acacia* plantations. Species such as long-tailed macaques used both non-*Acacia* and natural forest, and civets were common in both *Acacia* and non-*Acacia*. Western tarsiers and yellow-throated martens used both *Acacia* and natural forest.

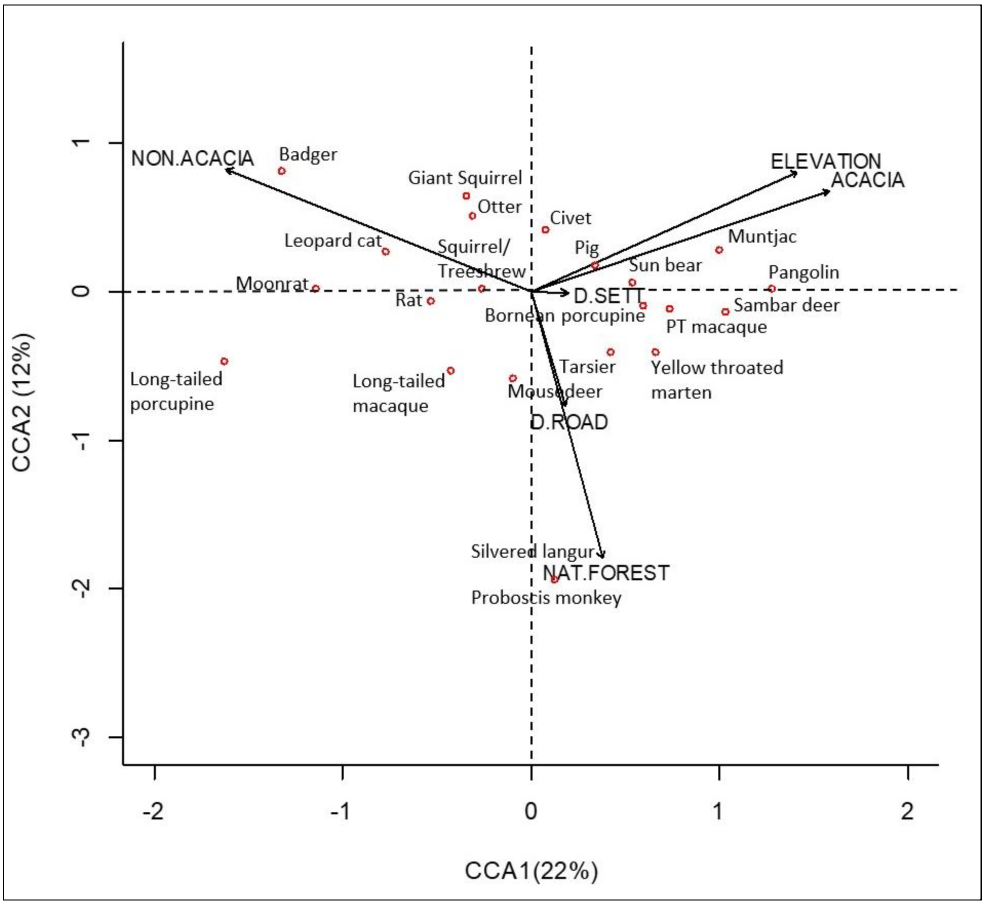

Figure 4: Canonical correspondence biplot (species detections and environmental variables) with six standardized environmental covariates based on mammal species surveys with remote cameras, Bengkoka Peninsula, Sabah, Malaysia, 2016–2017. Environmental covariates were area (ha) of natural forest, *Acacia* plantation, or non-*Acacia* plantation within a 500-m buffer radius (i.e., NAT.FOREST, ACACIA, NON.ACACIA, ELEVATION), distance to nearest settlement (D.SETT), and distance to nearest road (D.ROAD). The first two canonical axes explained 69% of the total variance in species data.

4.0 DISCUSSION

Our primary objective was to assess the relationship between habitat gradients and the community composition of mammals in a landscape mosaic of commercial plantations and natural forest. Based on the camera data and additional direct observations, we documented at least 34 species of native mammals in the study area, including several threatened species such as sun bears, Sunda pangolin, and sambar (Table S1). This finding contrasts with a 2009 report that considered no large mammals of conservation value to be extant in the area (KWEC, 2009). Rarefaction analyses suggest that species richness in natural forest and *Acacia* cover types was likely much greater than observed. Species richness of mammals was greatest in natural forest. Mammal detections increased with decreasing elevation and at greater distances from the nearest edge of *Acacia* plantations. Detections of threatened mammals increased with the area of natural forest and *Acacia*, and closer proximity to roads. Mammal diversity in non-*Acacia* forests was lowest, and included many small, generalist species. Larger mammals, including several threatened species, were associated with areas containing larger stands of *Acacia* and natural forest. It is not surprising that mammal use of natural forest patches would be high, but our results suggest that *Acacia* plantations also may possess attributes supporting a diversity of mammal species, including those we defined as threatened based on IUCN criteria.

Lowland forests support almost 90% of Peninsular Malaysia's mammal species with nearly 2/3 of those species confined to forests below 1,000 m (Lim, 2008). Although the elevational range of our study area was narrow (0–100 m), even minor changes in elevation can have dramatic effects on forest type and management. Indeed, natural forest and coastal mangrove remnants were at low elevations, and both were used intensively by mammals. Human access likely played a role as well. Although not all forest compartments were gated, human access to natural forest and *Acacia* stands was more restricted compared with non-*Acacia* areas, the majority of which were small holdings under private ownership. Human activities in *Acacia* plantations were limited mostly to forest management practices. Once seedlings reached 2–3 years, maintenance of the plantation was minimal. Also, apart from two major access roads, most plantation roads were subject to low levels of vehicular traffic.

Non-*Acacia* cover types, including young stands of *Eucalyptus pellita*, were more intensively managed with daily activities such as rubber-tapping, hand-pollination, weeding, fertilizing, and harvesting. Most of these were small holdings close to homesteads, domestic animals, and human settlements, and had no gates or security check points. Furthermore, landowners exercised little control over hunting in contrast to land managed by the *Acacia* plantation companies, which enforced a no-hunting policy. Therefore, our findings likely reflect the combined effects of human disturbance and exploitation on vulnerable species. Larger mammals are vulnerable to bushmeat hunting or for trade in wildlife parts (Carter et al., 2017), whereas small mammals such as western tarsiers are removed from the wild for the local and international pet trade (Shekelle and Yustian, 2008). The fact that overall mammal detections and larger-bodied mammals were associated with stands of *Acacia* and natural forest, and threatened mammal detections were associated with *Acacia* stands may owe mostly to lower levels of human disturbance in these cover types.

Numerous studies have shown the detrimental effects of roads on biodiversity because of increased access to hunters or poachers (Haines et al., 2012), higher rates wildlife-vehicle collisions, and facilitation of habitat loss and fragmentation through human encroachment (Fahrig and Rytwinski, 2009; Van Langevelde, 2009). Our finding that threatened mammal detections were greater near roads was therefore unanticipated. However, the road network in the study area consisted mostly of unpaved roads, and apart from two frequently used routes that connected the north-south and east-west regions of the peninsula, vehicular traffic was low. Also, some species habitually use old logging roads and unpaved roads (Slater, 1994; Weckel et al., 2006; Bitetti et al., 2014; Kolowski and Forrester, 2017), possibly because the open habitat facilitates travel, provides resources along road edges, or reduces predation risk.

We did not account for false absences, thus species richness and detection rates among different types of land-use likely are underestimates. Species accumulation curves in *Acacia* and natural forest did not reach asymptotes, suggesting that increased sampling intensity would reveal greater species richness than we observed. Cameras were deployed for 21 sampling occasions at each site, a sampling period that we considered sufficient to capture the occurrence of most mammal species within a 500-m radius of the camera. However, species differ in how they move around within their home range and one camera per sampling location may be insufficient to capture the range of species that use the area, particularly species that are primarily arboreal or fossorial. Increasing the number of cameras per sampling location (multiple camera arrays) and varying camera positions may be more effective to increase detection rates than extending the length of the sampling period, particularly for species with low detection probabilities (O'Connor et al., 2017).

We attempted to improve detection rates by using a scent lure. This might have introduced some bias by possibly attracting some species more than others (Kays and Slauson, 2008). Nevertheless, the use of scent lures may enhance detections of rare carnivores and maximize the probability that an animal close to the camera will be photographed (Holinda et al. 2020). We found that a variety of mammals, including omnivores and herbivores, investigated the lure. Furthermore, because the quantity of lure was small, it is unlikely that individuals were attracted to the site beyond the estimated sampling radius of ~500 m. Detections of some species may have been biased low, also, because of where cameras were placed. We consistently placed cameras about 40 cm from ground level, which may have reduced detectability of primates and species like palm civets that are highly arboreal. For example, we obtained no camera records of the following arboreal species, even though they were occasionally seen or heard: red langurs (*Presbytis rubicunda*), the Bornean gibbon (*Hylobates muelleri*), slow loris (*Nycticebus borneanus*), and short-tailed mongoose (*Herpestes brachyurus*; Table S2).

A curious feature of our results was that camera detections of threatened species such as sambar, sun bear, and pig-tailed macaques were greater in natural forest, but ordination and regression analyses, which accounted for the total area of different vegetation types within a 500-m radius around sample sites, associated these species with *Acacia* forests. The likely explanation is that most natural forest in the study area consisted of narrow strips (20–50 m) along streams and drainages, and cameras placed at these locations had a buffer composed mostly of *Acacia*. With the exception of bearded pigs, western tarsiers, muntjac, civets, and a few other species, detections of all other species were greater in natural forest, indicating that this habitat, including its mosaic nature, may be crucial for maintaining mammal diversity in plantation forests. *Acacia mangium* is an aggressive invader and without intervention, its regeneration from seeds may ultimately erode and overcome small remnants of natural forest (Koutika and Richardson 2019). Our results predict that such an outcome may cause reductions in species richness, including the failure to support some threatened species.

As industrial plantations expand, finding ways to mitigate the loss of biodiversity is critical. Mang and Brodie (2015) reported that species richness of multiple taxa in *Acacia* plantations was about 47% that of intact forests. A notable feature of the Bengkoka study area was its relative isolation from large intact forests, yet species richness (n = 22) was comparable to those reported from studies conducted in much larger plantation landscapes with large proportions of secondary forest and greater sampling intensity (n = 20 species; >5000 sampling occasions; McShea et al., 2009), plantations adjacent to national parks (n = 21; Yaap et al., 2016) and surveys in natural forest in Borneo (n = 24-27, Bernard et al. 2013, 2014; n = 15, Mohd-Azlan and Lading, 2006). Samejima et al. (2012) reported 33 species in intact forests, Deramakot, Sabah, but with ~10 × the sampling occasions of our study. However, none of the surveys in natural forests used scent lures, whereas those conducted in plantations did. Although detections were few, several threatened species persist in the Bengkoka study area, including the Critically Endangered Sunda pangolin, Endangered proboscis monkey, Vulnerable western tarsier and Near-Threatened silvered langur. Apart from this study, the western tarsier was reported only in Samejima et al.'s (2012) study. Remarkably, Bengkoka peninsula is about 1/20th the size of the 4900 km^2 area of Sarawak's Planted Forests Project. The latter retains ~39% of its area in secondary forest (McShea et al., 2009) in stark contrast with <18% in Bengoka. Patches of mangrove forests occurred along the Bengkoka coastline, including fringes of the study area, which may have influenced the persistence of the proboscis monkey, silvered langur, western tarsier, and many other species that are rare in inland forests. Although we did not include distance to the coastline as a covariate in our analyses, prediction maps for species richness and overall mammal detections indicated higher values for areas close to the coastal mangrove habitat.

About 40 years ago, substantial areas of Bengkoka peninsula were converted to industrial plantations, but we have no data on faunal communities at the time. At the time of our study, the landscape was dominated by *Acacia mangium*, but contained patches of oil palm, rubber, and rice plantations, fragments of secondary forest, coastal mangroves, and young *Euclayptus pellita* stands. The area still supports valuable elements of mammal diversity including a number of threatened species that so far have persisted and adapted to substantial landscape changes over four decades. Our study demonstrates that natural forest patches are important for almost all native mammals, but the remnants in this managed landscape were sparse. Retaining and expanding these areas through restoration will positively improve mammal diversity and persistence. Restoration of fallow areas with native trees such as fig (*Ficus* spp.), oak (*Lithocarpus* spp.,), *Castanopsis* spp., and *Artocarpus dadah* would improve habitat conditions for a range of frugivores, including sun bears.

Since the 1980s, *Acacia mangium* has been the species of choice for commercial timber plantations in Malaysian Borneo with the largest area of planted forests in the state of Sarawak (403,017 ha), followed by Sabah (300,521 ha; Lee, 2018). Plantations are much more extensive in Indonesia and Vietnam (McBeth, 2014; Kien et al., 2014). Fungal diseases with no effective means of control now pose the most significant challenges to *Acacia* plantations in Southeast Asia, with large landholdings already converted to *Eucalyptus pellita* in Indonesia and transitions underway in Sabah and Sarawak (Lee 2018), including the Bengkoka Peninsula. *Eucalyptus* stands may ultimately prove suitable for species that currently use *Acacia* stands, such as bearded pig, western tarsier, sambar, and sun bear. Data on mammalian diversity in *Acacia* and *Eucalyptus* plantations in Borneo remain sparse. Longitudinal studies that monitor wildlife responses and population change, rather than presence/absence, will help evaluate the resilience of different species of mammals to changes in managed forest landscapes. The configuration of natural forest remnants, also, and their connectivity to source habitats such as national parks and forest reserves, have an important influence on mammal communities in plantation forests (e.g., Cheyne et al., 2016, Yaap et al., 2016). Such information will be crucial to facilitate management objectives for conserving mammal diversity.

The tendency for threatened mammals to be found near roads in the study area merits attention. The current road network consists primarily of unpaved roads with limited or restricted use. Informal interviews with local villagers confirmed that wildlife hunting for sambar deer, bearded pig, and sun bear occurred in the study area and were traded in Bengkoka Peninsula. On plantation lands, enforcing speed limits near roads, patrolling, vehicle checks at entrances, and spot-checking for snares near roads may help mitigate these risks. Such enforcement may be difficult in other parts of the peninsula with public access. The chief challenge of roads facilitating poaching thus remains and is emblematic of one of the greatest threats to wildlife in Southeast Asia (Corlett, 2007; Gray et al., 2018). Public awareness and outreach campaigns will be extremely important to build local support to conserve the mammalian biodiversity that still exists in the area.

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Supplementary Information

Table S1. Species of mammals detected with remote cameras (2016–2017) and field surveys, Bengkoka Peninsula, Sabah, Malaysia, 2016–2018. IUCN status (IUCN 2019): CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concerned.

	Family/ Species	Common name	IUCN status	Diet	Body mass (kg)
	Bovidae				
1	*Bubalus bubalis*	Feral water buffalo	-	H	950.0
	Canidae				
2	*Canis lupus familiaris*	Feral dog	-	O	15.0
	Cercopithecidae				
3	*Nasalis larvatus*	Proboscis monkey	EN	H	18.0
4	*Macaca nemestrina*	Pig-tailed macaque	VU	H	6.5
5	*Macaca fascicularis*	Long-tailed macaque	LC	O	5.0
6	*Presbytis rubicunda* [c]	Red langur [c]	LC	H	6.3
7	*Trachypithecus cristatus*	Silvered langur	NT	H	5.3
	Tarsiidae				
8	*Tarsius bancanus*	Western tarsier	VU	C	0.2
	Cervidae				
9	*Rusa unicolor*	Sambar deer	VU	H	200.0
10	*Muntiacus muntjak*	Red muntjac	LC	H	24.0
	Erinaceidae				
11	*Echinosorex gymnura*	Moonrat	LC	C	1.0
	Felidae				
12	*Pardofelis marmorata* [b]	Marbled cat [b]	NT	C	3.8
13	*Prionailurus bengalensis*	Leopard cat	LC	C	2.5
14	*Felis catus*	Feral cat	-	C	4.0
	Herpestidae				
15	*Herpestes* spp. [d]	Mongoose species [d]	NT	C	1.3

	Hylobatidae				
16	*Hylobates muelleri* [a]	Bornean gibbon [a]	EN	H	6.0
	Hystricidae				
17	*Hystrix crassispinis*	Bornean porcupine	LC	O	2.0
18	*Trichys fasciculata*	Long-tailed porcupine	LC	O	2.0
	Lorisidae				
19	*Nycticebus menagensis* [d]	Slow loris [d]	VU	O	0.5
	Manidae				
20	*Manis javanica*	Sunda pangolin	CR	I	4.8
	Mephitidae				
21	*Mydaus javanensis*	Malay badger	LC	O	2.5
	Muridae				
22	-	Rat species	-	-	-
	Mustelidae				
23	*Aonyx cinereus*	Small-clawed otter	VU	C	3.3
24	*Lutrogale perspicillata*	Smooth-coated Otter	VU	C	9.0
25	*Martes flavigula*	Yellow-throated marten	LC	O	1.4
	Nycteridae				
26	-	Bat species	-	-	-
	Sciuridae				
27	*Lariscus hosei*	Four-striped ground squirrel	LC	H	0.2
28	*Ratufa affinis*	Pale giant squirrel	NT	H	1.2
29	*Callosciurus notatus*	Plantain squirrel	LC	O	0.2
	Suidae				
30	*Sus barbatus*	Bearded pig	VU	O	122.5
	Tragulidae				
31	*Tragulus* spp.	Mousedeer species	LC	H	3.3
	Tupaiidae				
32	*Tupaia glis*	Common treeshrew	LC	I	0.2
33	*Tupaia gracilis*	Slender treeshrew	LC	I	0.1

Table S1. (Continued)

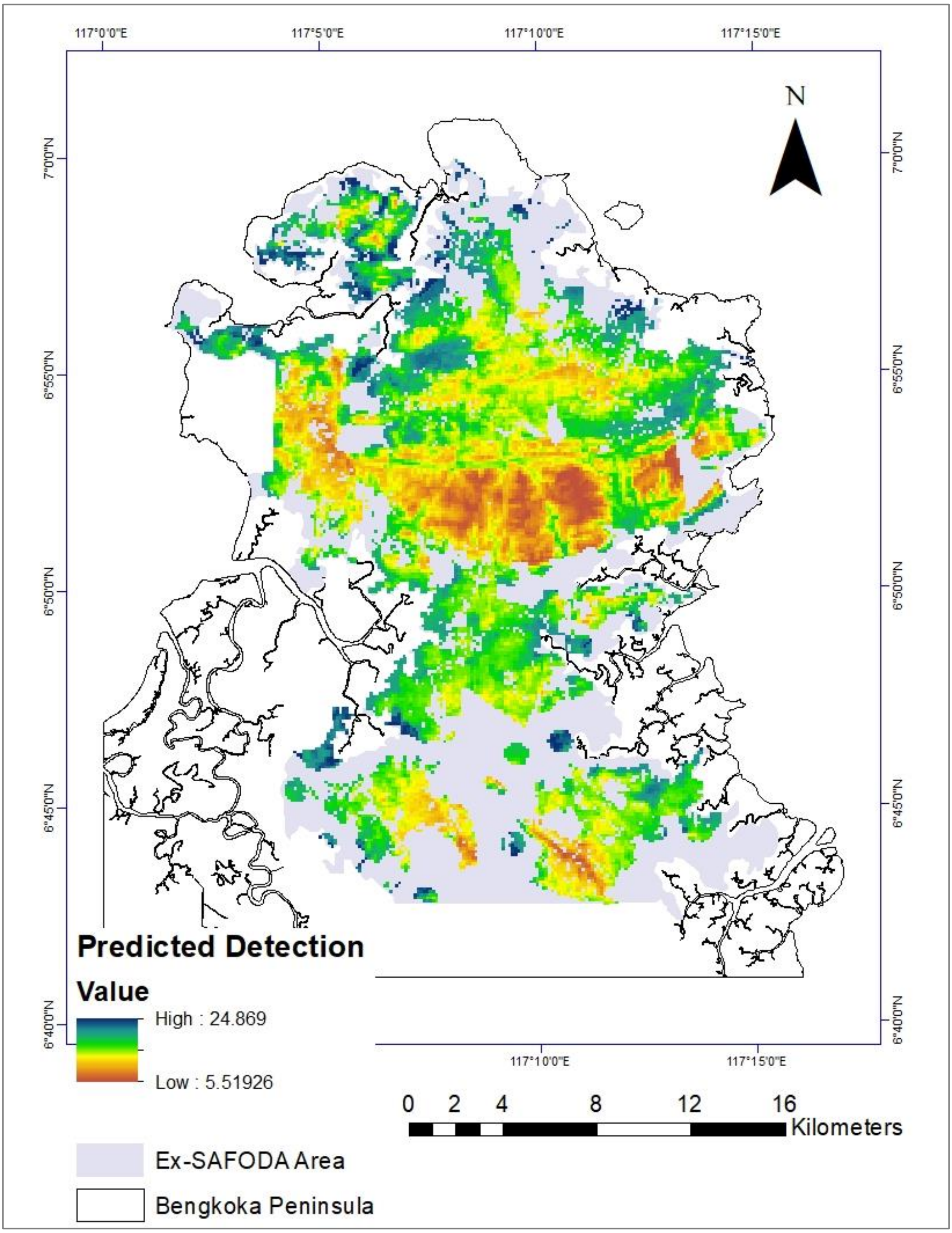
	Family/ Species	Common name	IUCN status	Diet	Body mass (kg)
34	*Tupaia minor*	Lesser treeshrew	LC	O	0.1
	Ursidae				
35	*Helarctos malayanus*	Sun bear	VU	O	42.5
	Viverridae				
36	*Paradoxurus hermaphroditus*	Common palm civet	LC	O	2.5
37	*Viverra tangalunga*	Malay civet	LC	O	3.9

[a] call heard

[b] detected by camera trap after the sampling period

[c] sighted

[d] carcass found

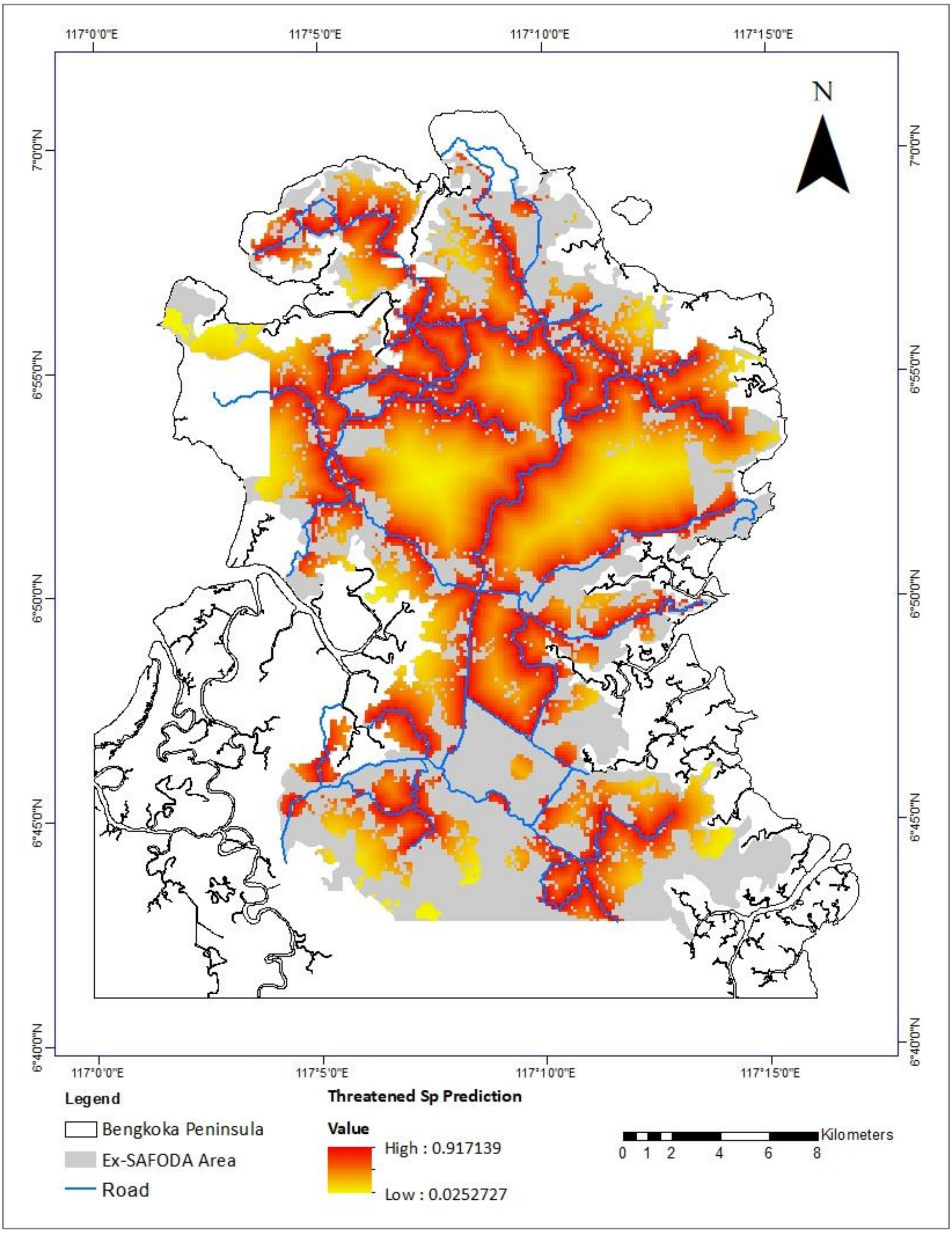
776 

777 **SFigure 1.** Predictions of mammal detections based on averaged parameter estimates of regression

778 models, Bengkoka Peninsula, Sabah, Malaysia, 2016–2017. Predictions have been applied only to parts

779 of the study area for which land use data were available.

780



SFigure 2. Predictions of threatened mammal detections based on averaged parameter estimates of regression models, Bengkoka Peninsula, Sabah, Malaysia, 2016–2017. Predictions have been applied only to parts of the study area for which land use data were available.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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