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Original investigation

Fine-scale distributions of carnivores in a logging concession in Sarawak, Malaysian Borneo

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ABSTRACT

Coarse-scale patterns of distribution and abundance of species are the outcome of processes occurring at finer spatial scales, hence the conservation of species depends on understanding their fine-scale ecology. For Bornean carnivores, little is known about fine-scale predictors of species occurrence and it is assumed that the two main threats to wildlife on Borneo, habitat disturbance and hunting, also impact their occurrence. To increase our understanding of the Borneo carnivore community, we deployed 60 cameras in a logging concession in northern Sarawak, Malaysian Borneo, where different landscape covariates, both natural and anthropogenic, were present. We built single-species occupancy models to investigate fine-scale carnivore occupancy. Overall, forest disturbance had a negative effect on Hose's civet (*Diplogale hosei*), banded civet (*Hemigalus derbyanus*) and yellow-throated marten (*Martes flavigula*). Further, banded civet had greater occupancy probabilities in more remote areas. Logging roads had the most diverse effect on carnivore occupancy, with Hose's civet and masked palm civet (*Paguma larvata*) negatively affected by roads, whereas Malay civet (*Viverra tangalunga*), short-tailed mongoose (*Herpestes brachyurus*) and leopard cat (*Prionailurus bengalensis*) showed higher occupancy closer to roads. Canopy height, canopy closure, number of trees with holes (cavities) and distance to nearest village also affected occupancy, though the directions of these effects varied among species. Our results highlight the need to collect often overlooked habitat variables: moss cover and 'kerangas' (tropical heath forest) were the most important variables predicting occurrence of Hose's civet. The preservation of such forest conditions may be crucial for the long-term conservation of this little-known species. Our results confirm that logged forests, when left to regenerate, can host diverse carnivore communities on Borneo, provided less disturbed habitat is available nearby, though human access needs to be controlled. We recommend easy-to-implement forest management strategies including maintaining forest next to logging roads; preserving fruiting trees and trees with cavities, both standing and fallen; and blocks of remote, less disturbed, mid- to high-elevation forest with understorey vegetation.

Introduction

The islands of Southeast Asia are recognized as global biodiversity hotspots (Myers et al., 2000) and within insular Southeast Asia, Borneo is recognised as an evolutionary hotspot hosting high levels of mammalian species richness and endemicity (de Bruyn et al., 2014). Borneo currently suffers high levels of deforestation, losing its forest cover at nearly twice the rate of the rest of the world's humid tropical forests. Within the last four decades, over 30% of Borneo's forests were cleared (Gaveau et al., 2014). Of the geopolitical units on Borneo, the Malaysian state of Sarawak has the least proportion of intact forest remaining at 14.6% compared to 19.1% in Sabah, 32.6% in Kalimantan and 56.9% in Brunei (Gaveau

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et al., 2014). The coverage of protected areas in Sarawak remains low at 4.2% of total land area (DOS, 2011). Much of the forest loss and degradation in Sarawak has been due to logging, as evidenced by the greatest density of logging roads on Borneo (Gaveau et al., 2014). Moreover, only one logging concession in Sarawak is currently certified as sustainably managed by the Malaysian Timber Certification Scheme. In contrast to other provinces on Borneo, no logging concession has been certified by the international Forest Stewardship Council (Mathai et al., 2016a).

In addition to habitat conversion, degradation and fragmentation, hunting is a serious threat to many mammals on Borneo (e.g. Bennett et al., 2000; Brodie et al., 2015a), presumably including carnivores. Hunting may be a larger problem in Sarawak and Kalimantan than in Brunei and Sabah because of larger populations of forest- and wildlife-dependent indigenous communities (Bennett et al., 2000). The effects of hunting and wild meat consumption on Bornean carnivore populations are largely unknown (Mathai et al., 2016a), though illegal hunting and wildlife trade are increasing (Shepherd et al., 2011).

Twenty-five carnivore species occur on Borneo including more endemics than any other island except Madagascar (Shepherd et al., 2011). About half of these carnivores are classified by The IUCN Red List of Threatened Species as globally threatened (IUCN, 2016) with little available information on their basic ecology and tolerance to habitat disturbance (Mathai et al., 2016a). Additionally, most studies conducted in Borneo, and particularly in Sarawak, were focussed on coastal areas and lowland forests due to easier logistics, resulting in little information on highland species. Recently, some understanding of coarse-scale distribution of many carnivore species within Borneo was achieved (Mathai et al., 2016a), but fine-scale predictors of species persistence are lacking, with few studies addressing the effects of physical and anthropogenic covariates on Bornean carnivores. Fine-scale ecological studies provide the context and basis for studying processes and resultant patterns of distribution, abundance, diversity and interactions of species (Landres et al., 1999). Because animals often select resources differently at different scales, habitat associations found in distribution-wide studies cannot necessarily be translated to small-scale distribution of individuals (e.g., Boyce, 2006; Mayor et al., 2009). Bornean carnivores are ecologically diverse (i.e. different forest type, trophic niche, response to anthropogenic disturbances) and functionally important (i.e. as seed dispersers (Nakashima et al., 2010) and top predators), and thus, may be good indicators of the performance of different management and conservation strategies.

We analysed fine-scale distributions of carnivores within the Sela'an Linau Forest Management Unit (SL FMU), a logging concession in interior Sarawak, comprising lowland, upland and montane forest, the last two being little-studied forest types. We used an occupancy framework to investigate the role of habitat quality (i.e. vegetation structure) and anthropogenic factors such as logging, forest disturbance, distance to logging roads and human settlements and hunting. We then applied our results to forest management applications to facilitate the long-term conservation of the carnivore community in logging concessions.

Methods

Study area

The SL FMU (3°11′–29′N; 115°00′–20′E) is a logging concession of 55,949 ha in the Upper Baram region of interior northern Sarawak (Fig. 1A). The FMU's terrain is undulating with elevations from 250 m to 2000 m above sea level (a.s.l.). It receives high rainfall (3400–5900 mm annually) without distinct seasonality. The FMU supports mixed dipterocarp forest (60%), with some upper montane forest at higher elevations (4%). 'Kerangas' forest, which develops on nutrient-deficient soil and is less suitable for agriculture, covers 21%. This forest type is scattered on Borneo from the coast to more than 1000 m a.s.l (Brunig, 1974; see also Table 2); in our site, upland kerangas forests are common. Old and current shifting agriculture ('temuda') covers 15% of the study area. About half the area was logged conventionally (CL, high impact logging typically characterised by destructive log extraction techniques, liberal harvesting limits and rapid rotations) in the 1990s, and since 2003, reduced impact logging (RIL, less detrimental to forest structure and providing economically viable timber harvests over longer time frames; Edwards et al., 2012) was applied. The FMU contains a large tract of forest (about 3000 ha) that burned during the 1997–1998 El Niño event and where enrichment planting (with commercially-valuable, native species) has since been practised. Logging roads dissect parts of the FMU. The SL FMU lies in the Kelabit Highlands, with Pulong Tau National Park at its north-east border. It is part of the larger Heart of Borneo initiative, a government-led and NGO-supported agreement signed between Brunei, Malaysia and Indonesia to manage sustainably the remaining forests in the centre of the island. The FMU is thus an important area for conservation and has been identified as an important site for carnivores (Mathai et al., 2010, 2016a).

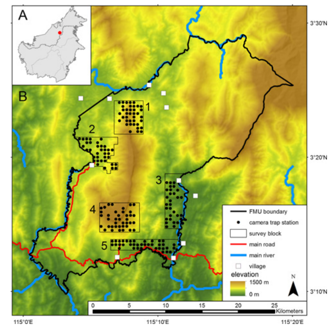

Fig. 1. Location of the Sela'an Linau Forest Management Unit (FMU) on Borneo (A). Locations of our five study blocks with camera arrays and locations of main roads, rivers and villages (B). Numbering of blocks follows descriptions in Table 1.

In the FMU live many indigenous human communities such as the Kayan, Kelabit, Kenyah and Penan, who depend on forest and wildlife for their livelihoods. Local hunters from these communities do not actively target small carnivores, their preferred quarry being ungulates and primates, though indiscriminate hunting techniques e.g. the use of snares and traps, may still impact the more ground-dwelling carnivores (Mathai et al., 2010). The FMU was the first of only two logging concessions in Sarawak to be certified under the old Malaysian certification scheme for sustainable forest management. It lost this certification in 2009, mainly due to unsettled issues with native communities. The concessionaire did not pursue re-certification and logging activities have since declined markedly.

Sampling design

Camera trapping

Field work was conducted between April 2013 and August 2014. Logistical challenges due to remoteness of the forest and difficult terrain, as well as lack of cooperation from some indigenous communities, prevented covering the entire SL FMU as one sampling unit. Therefore, we chose five sampling blocks within the FMU for our camera-trap surveys (Fig. 1B) representing the range of elevation, logging regime, proximity and density of logging roads and settlements, and differences in forest disturbance and hunting pressure (where forest disturbance was assessed through survey-

Table 1
Survey blocks from the camera trapping study in the Sela'an Linau Forest Management Unit, Sarawak, Malaysian Borneo. Numbering follows Fig. 1.

Block	Elevation range of cameras (m)	Main forest type and anthropogenic disturbance[a]
1. Protected Zone LL (PZ LL)	570–1200	Unlogged forest, mainly highland kerangas, with low anthropogenic disturbance; surrounded at lower elevations by four indigenous villages along the Tutoh river, with forest affected by shifting agriculture of various ages and moderate to high hunting pressure.
2. C1	500–900	Mainly regenerating forest, logged between 2006 and 2008 using RIL methods; old logging roads, one indigenous village, some shifting agriculture and moderate hunting pressure; some highland kerangas.
3. Sel	250–560	Unlogged forest; some anthropogenic disturbance due to four indigenous villages and shifting agriculture of various ages, particularly along the Selungoh river, with high hunting pressure.
4. Protected Zone Kel (PZ Kel)	750–1550	Unlogged forest, mainly highland kerangas, with low anthropogenic disturbance.
5. BZ	250–750	Along the main, active logging road; conventionally logged in the early 1990s and then affected by fires during the 1997–98 El Niño event; some shifting agriculture, silvicultural treatment; high hunting pressure and anthropogenic disturbance.

[a] Anthropogenic disturbance at each block was assessed through surveyors' observations and discussions with logging company staff and local communities, considering logging history, extent of shifting agriculture and human settlements and extent of damage by forest fires; relative hunting pressure at each block was assessed qualitatively through the surveyors' observations and personal communication with indigenous hunters.

ors' observations and discussions with logging company staff and local communities, considering logging history, extent of shifting agriculture and human settlements, and extent of damage by forest fires; and relative hunting pressure at each block was assessed qualitatively through the surveyors' observations and personal communication with indigenous hunters; see Table 1). Each block covered 15–20 km^2 and 40 camera trap stations were set up per block at least 500 m apart. We chose 500 m as a compromise between logistical feasibility and satisfying the assumption of spatial independence in occupancy models by exceeding the home range size of most target species (MacKenzie et al., 2006); sun bear *Helarctos malayanus* and Sunda clouded leopard *Neofelis diardi* were excluded from the analysis due to their known larger home ranges. At each block, we sampled 20 points with two Reconyx Hyperfire HC500 cameras (both cameras placed within a 50 m radius of centre point, facing different trails in opposite directions) and the other 20 points with a single camera to optimally use the available 60 cameras and maximise detection probability while accounting for logistical difficulties. We used locally available fish oil as a lure. Because we estimated detection probability for each species in the occupancy models, we did not expect usage of lures to impact our results; lures would only impact detectability and not occupancy itself as it is unlikely that animals could smell the lure greater than 150 m (transect length for vegetation surveys) from the camera trap station. After the last camera set in a block accumulated 45 trap-nights, we moved all cameras to the next block.

Habitat surveys

We characterised the habitat surrounding each camera trap station to assess the general forest structure and disturbance using three 150 m line transects oriented 0°, 120° and 240° from each centre point and pooled the data of the three transects. Along each transect, we recorded seven measurements of habitat structure and four variables pertaining to predominant forest type/land use history at each station (Table 2).

Data analysis

We conducted all analyses in R 3.2.0 (R Core Team, 2015). We used package *camtrapR* (Niedballa et al., 2016) for initial data preparation. We pooled data from camera trap images into 8-day occasions resulting in a minimum of six sampling occasions. In each occasion, we calculated trap effort (number of active camera trap-nights per station per occasion) and where two cameras were placed at a station, we summed the trap-nights for the two cameras, as the two cameras were set on different trails and therefore were operationally independent, though spatially dependent. We constructed detection-nondetection matrices for all stations and occasions. Assuming all carnivore species had similar associations with different habitat variables across the five study blocks, we joined the dataset from all blocks and modelled occupancy for this joint data set. Because there are no strong seasonal differences in Sarawak and no evidence of carnivore migrations on Borneo, we do not expect the timing of the surveys to affect carnivore occupancy or habitat associations. To examine what influenced carnivore occupancy in our landscape, we constructed occupancy models which estimate the probability of occurrence of a species at a station while accounting for imperfect detection (MacKenzie et al., 2006). Both occupancy probability and detection probability can be modelled as functions of covariates. We first modelled variation in detectability by constructing a set of candidate models where the probability of detection of carnivores was modelled as either a function of trapping effort (as defined above) or as a constant. We did not use block as a covariate on detection as it represented differences in forest disturbance, logging history, elevation, distance to roads, rivers and villages and hunting pressure and thus, could have masked the effects of other covariates on occupancy. Conditional on the best detection model (see model selection below), we then modelled carnivore occupancy by testing a set of covariates collected in-situ and covariates derived from regional or global GIS datasets (see Table 2 for details), first using covariates individually, then using combinations of important covariates. To investigate the effects of logging, we combined stations that were harvested using both RIL and CL methods because sample sizes were too small to investigate each treatment separately. Similarly, too few stations were affected by forest fires and shifting agriculture and therefore, we created a composite covariate, disturbance. Another composite variable, distance to accessibility (d_access) was created, capturing the distance of each station to the nearest main/secondary logging road, main river or village, whichever was nearest, as a proxy of human access and potential for hunting activity (Table 2). Occupancy models were implemented in R using package *unmarked* (Fiske and Chandler, 2011).

We standardised all continuous variables to have mean = 0 and variance = 1. All continuous variables were tested for collinearity using Spearman's rank correlation and were not included in the same model if substantially correlated (coefficient > 0.7; Dormann et al., 2013). For each species, we constructed models representing combinations of the occupancy covariates, ensuring that the ratio of sample size *(n)* to parameters *(k)* was ≥10 by considering only models with a limited number of parameters, thereby avoiding overparameterisation (a full list of candidate models can be found in Appendix A). We based model selection on Akaike's information criterion (AIC) using *unmarked* and used AIC differences and Akaike weights to assess the explanatory power of each model relative to the others. We considered all parameters that occurred in

Table 2
Covariates used for occupancy modeling of carnivores detected in the Sela'an Linau Forest Management Unit, Sarawak, Malaysian Borneo. Covariates were measured in-situ or were calculated in R 3.2.0 using local and global GIS datasets. Covariates in italics were not used in the final model as these were summarised into composite covariates. Covariates that were correlated (slope and ruggedness; d_village and d_access) and those derived from other covariates (d_access from d_village, d_road and d_water) were not used in the same model.

Covariate	Description
Median diameter at breast height, DBH[a]	All trees >10 cm DBH within 2 m of the transect
Median canopy height, CH[a]	Measured at 25 m intervals along each transect using clinometer
Mean canopy closure, CC[a]	Measured at 50 m intervals along each transect using spherical desiometer Canopy closure refers to the proportion of the sky hemisphere obscured by vegetation when viewed from a single point (Jennings et al., 1999).
Mean understorey vegetation density, UVD[a]	Used (1.5 × 1 m) checkerboard with 150 (0.1 × 0.1 m) cells, with 4 equally spaced dots of identical size within each cell. Checkerboard was photographed at 50 m intervals along each transect at distance 10 m from either side of transect line and number of dots covered by vegetation was expressed as a fraction of total dots.
Mean moss cover, M[a]	Visual observation along a gradient 0 (no moss) to 4 (full moss cover), recorded at 25 m intervals along each transect.
number of boulders, B[a]	Number of boulders >50 cm along each transect
number of trees with holes (cavities), TH[a]	Number of trees (both standing and fallen) with cavity opening > 20 cm along each transect.
logged[a]	*Was forest around a station unlogged, logged by RIL or logged by CL? [3 levels: 'unlogged', 'logged_RIL' and 'logged_CL']*
Logging	Composite variable combining points harvested using both RIL and CL (from covariate 'logged') [2 levels: 'logged' and 'unlogged']
burnt[a]	*Was forest around a station affected by forest fires of the 1997–1998 El Niño event (measured within the transect distance of 150 m around the station)? [2 levels: 'burnt' and 'unburnt']*
temuda[a]	*Was forest around a station formerly subject to shifting agriculture (measured within the transect distance of 150 m around the station)? [2 levels: 'temuda' and non temuda]*
Disturbance	Composite variable combining covariates 'logging', 'burnt' and 'temuda' [2 levels: 'disturbed' and 'undisturbed']
Kerangas[a]	Kerangas means 'land that cannot grow rice' in the native Iban language. It refers here specifically to highland kerangas found on Borneo. These are upland forests characterised by infertile, sandy soils, presence of epiphytic plants (e.g. Nepenthes), streams with reddish water and typically on sandstone outcrops (Brunig, 1974). [2 levels: 'kerangas' and 'non kerangas']
distance to nearest village (d_village) distance to nearest road (d_road) distance to nearest water source (d_water)	Euclidean distance to nearest village, road (main/secondary/feeder) and water source (river/stream/lake) from each station. Location data provided by the logging concessionaire
distance to accessibility (d_access)	Composite variable capturing minimum of distance to village, main/secondary road and main river, from each station.
Slope Aspect ruggedness	Calculated from the 90 m SRTM digital elevation model (DEM, http://srtm.csi.cgiar.org)
topographic position index (TPI)	TPI is the elevational difference between each cell of the DEM and the mean elevation of its eight neighbours.

[a] Measured/recorded in-situ.

models within two units of ΔAIC of the top model of each species as important in explaining occupancy of that species. To visualise habitat associations, we plotted response curves based on the top model for each species, showing standard errors and 95% confidence intervals.

Results

After accounting for camera failure and thefts, we retrieved data from 179 stations. We recorded 498 independent events (photographs of the same species at the same station, where a station consists of either one or two cameras, within 60 min, were considered the same 'event') of 15 carnivore species over 14,814 camera trap nights. Of these species, banded civet *Hemigalus derbyanus* was the most commonly recorded and widespread, being detected 142 times at 69 stations (Table 3). We had sufficient records to build occupancy models for seven species (Tables 3 and 4). Banded civet, Hose's civet *Diplogale hosei*, masked palm civet *Paguma larvata*, leopard cat *Prionailurus bengalensis* and yellow-throated marten *Martes flavigula* were detected across almost all blocks, though more often in the less disturbed, higher elevation forests of the Protected Zone (PZ), with Hose's civet records being almost exclusively from the PZ (Table 3). Malay civet *Viverra tangalunga* and short-tailed mongoose *Herpestes brachyrus*, though recorded from all blocks, were detected more often in the recently logged C1, with the latter also recorded regularly in the areas affected by forest fires.

Masked palm civet exhibited the highest occupancy (0.64 ± 0.16), whereas yellow-throated marten had the lowest occupancy (0.08 ± 0.05) of the seven species. For all species but masked palm civet, multiple models fell within two units of ΔAIC of the top model, suggesting similar support for these models. In most cases, one or two covariates were consistently represented in these similarly supported models, and consistently had coefficients whose confidence intervals did not include 0, indicating that these factors were important predictors for occupancy (Table 4). Banded civet occupancy was strongly related to understorey vegetation density (UVD) and d_access; Malay civet and short-tailed mongoose occupancy was strongly affected by distance to road (d_road) and canopy closure (CC); Hose's civet occupancy responded strongly to moss cover (M) and kerangas. The single top model for masked palm civet (next best model >5 AIC units from top model) included number of trees with holes/cavities (TH), d_road and distance to village (d_village). Leopard cat occupancy was influenced strongly by d_village and UVD; and occupancy of yellow-throated marten was strongly affected by canopy height (CH, Table 4). Direction and strength of these covariate relationships are depicted in Fig. 2.

Table 3
Carnivore species detected using cameras in the Sela'an Linau Forest Management Unit, Sarawak, Malaysian Borneo from April 2013 to August 2014. Basic information of the records is listed. Occupancy estimates are given for only the seven species for which we had sufficient records to build occupancy models. Occupancy estimates are derived from the top model in Table 4 and averaged over all stations.

Species	IUCN Red Listing[a]	Total number of independent events	Number of independent events in each block (refer to Table 1 for block descriptions)					Elevation range (m)	Naïve occupancy	Occupancy (S.E.) [95% C.I.][b]
			PZ LL	C1	Sel	PZ Kel	BZ			
Banded civet *Hemigalus derbyanus*	NT	142	48	17	10	41	26	260–1500	0.39	0.61 (0.08) [0.44–0.75]
Malay civet *Viverra tangalunga*	LC	67	4	29	12	11	11	260–1150	0.21	0.31 (0.08) [0.17–0.49]
Short tailed mongoose *Herpestes brachyurus*	NT	56	8	19	12	0	17	260–1370	0.18	0.24 (0.06) [0.13–0.38]
Hose's civet *Diplogale hosei*	VU	53	30	4	1	17	1	370–1500	0.16	In Kerangas: 0.32 (0.09) [0.17–0.52] In Non Kerangas: 0.07 (0.04) [0.02–0.21]
Masked palm civet *Paguma larvata*	LC	46	15	6	5	17	3	280–1500	0.18	0.64 (0.16) [0.31–0.87]
Leopard cat *Prionailurus bengalensis*	LC	30	1	0	1	22	6	260–1500	0.10	0.14 (0.06) [0.05–0.31]
Yellow-throated marten *Martes flavigula*	LC	19	6	1	2	7	3	290–1470	0.08	0.08 (0.05) [0.02–0.23]
Sun bear *Helarctos malayanus*	VU	48	9	12	1	16	10	260–1500	0.17	
Binturong *Arctictis binturong*	VU	13	5	1	0	5	2	275–1180	0.06	
Collared mongoose *Herpestes semitorquatus*	NT	9	2	0	0	0	7	245–1065	0.03	
Banded linsang *Prionodon linsang*	LC	4	0	0	0	4	0	1200–1550	0.02	
Marbled cat *Pardofelis marmorata*	NT	4	0	2	1	0	1	560–700	0.02	
Sunda clouded leopard *Neofelis diardi*	VU	3	3	0	0	0	0	1065–1180	0.01	
Bornean bay cat *Catopuma badia*	EN	3	0	0	0	3	0	1040–1210	0.01	
Malay weasel *Mustela nudipes*	LC	1	0	0	0	1	0	860	0.01	

[a] LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered.
[b] Refers to the probability that a station is occupied by the species. S.E. = standard error; C.I. = confidence interval.

Table 4
Top models for the seven carnivore species detected in the Sela'an Linau Forest Management Unit for which occupancy models were built. Where ΔAIC < 2, all competing models are shown, otherwise only top five models.

	Model	ΔAIC	AIC weight	No. of parameters
Banded civet	p(effort)psi(**UVD** + **d_access** + CH)	0.00	0.143	6
	p(effort)psi(**UVD** + **d_access** + TH)	0.24	0.127	6
	p(effort)psi(**UVD** + **d_access** + TH + Disturbance)	0.41	0.117	7
	p(effort)psi(**UVD** + **d_access**)	0.68	0.102	5
	p(effort)psi(**UVD** + **d_access** + TPI)	1.20	0.079	6
	p(effort)psi(**UVD** + d_access + Kerangas)	1.30	0.075	6
	p(effort)psi(**UVD** + d_access + Disturbance)	1.69	0.062	6
	p(effort)psi(**UVD** + **Dist** + CH)	1.91	0.055	6
Malay civet	p(effort)psi(**d_road** + **CC** + *d_village*)	0.00	0.350	6
	p(effort)psi(**d_road** + **CC** + M)	1.96	0.131	6
	p(effort)psi(**d_road** + **CC**)	2.07	0.124	5
	p(effort)psi(**d_road** + **CC** + ruggedness)	2.48	0.101	6
	p(effort)psi(**d_road** + **CC** + Disturbance)	3.50	0.061	6
Short-tailed mongoose	p(effort)psi(**CC** + **d_road** + ruggedness)	0.00	0.241	6
	p(effort)psi(**CC** + **d_road**)	0.74	0.167	5
	p(effort)psi(**CC** + **d_road** + TPI)	1.53	0.112	6
	p(effort)psi(**CC** + **d_road** + UVD)	2.38	0.073	6
	P(effort)psi(**CC** + **d_road** + d_village)	2.60	0.065	6
Hose's civet	p(effort)psi(**M** + **Kerangas** + TH)	0.00	0.172	6
	p(effort)psi(**M** + **Kerangas** + CC)	0.44	0.138	6
	p(effort)psi(**M** + **Kerangas** + d_road)	0.65	0.124	6
	p(effort)psi(**M** + **Kerangas**)	0.84	0.113	5
	p(effort)psi(**M** + **Kerangas** + Disturbance)	1.57	0.079	6
	p(effort)psi(**M** + **Kerangas** + TPI)	1.93	0.066	6
Masked palm civet	p(effort)psi(**TH** + **d_road** + **d_village**)	0.00	0.806	6
	p(effort)psi(**TH** + **d_road** + CH)	5.54	0.051	6
	p(effort)psi(*TH* + **d_road**)	6.20	0.036	5
	p(effort)psi(**TH** + **d_road** + UVD)	7.07	0.023	6
	p(effort)psi(**TH** + **d_road** + logging)	7.31	0.021	6
Leopard cat	p(effort)psi(**UVD** + **d_village**)	0.00	0.429	5
	p(effort)psi(**d_village** + *d_road*)	1.65	0.188	5
	p(effort)psi(*UVD* + *TH*)	1.97	0.160	5
	p(effort)psi(d_village + TH)	3.28	0.083	5
	p(effort)psi(d_road + **TH**)	4.62	0.043	5
Yellow-throated marten	p(effort)psi(**CH** + *d_village*)	0.00	0.215	5
	p(effort)psi(**CH** + Disturbance)	0.68	0.153	5
	p(effort)psi(**CH** + d_road)	1.51	0.101	5
	p(effort)psi(**CH** + TH)	1.78	0.088	5
	p(effort)psi(**CH** + d_access)	2.27	0.069	5

Bold indicates 95% CI does not include 0 for this variable in this model.
Italics indicates 90% CI does not include 0 for this variable in this model.
Note: 95% CIs for effort do not include 0 for all species except leopard cat and yellow-throated marten; for these two species, 95% CI includes 0 for all models.

Distance to roads affected occupancy of all species except banded civet (Table 4) but the direction of this effect varied between species. Similarly, the directions of effects of other environmental variables (e.g. canopy height, canopy closure, number of trees with holes (cavities)) varied between species. Detailed parameter estimates for models listed in Table 4 can be found in Appendix B.

Discussion

Anthropogenic disturbances such as logging alter forest structure and resource availability for mammals (Johns, 1988). This has been associated with changes in abundance of species (Bicknell and Peres, 2010); on Borneo, carnivores are the taxonomic group most negatively affected by logging (Brodie et al., 2015b). In our study, overall forest disturbance adversely affected occupancy of Hose's civet, banded civet, and to a lesser extent, yellow-throated marten, suggesting low tolerance to disturbed habitat, whether logged, or areas subject to shifting agriculture or forest fires. This result confirms current information on Hose's civet (Jennings et al., 2013; Mathai et al., 2016b) and banded civet (Jennings et al., 2013; Ross et al., 2015), but is partially contrary to the suggestion that yellow-throated marten is tolerant of degraded habitat across its range, including Borneo (Hon et al., 2016). Yellow-throated marten was recorded in our study from all forest blocks, including disturbed blocks. However, most records were from the mid- to higher-elevation forests of the Protected Zone (PZ) and at greater distances from villages. This species may experience higher hunting levels caused by higher conspicuousness, being diurnal and often moving in small groups (Grassman et al., 2005). Because the forests of the PZ are both less disturbed and less affected by hunting, our models were possibly unable to separate whether habitat disturbance or hunting impacted occurrence of this species.

Our models suggested that logging had no effect on occupancy of carnivores in our site, similar to Brodie et al. (2015a) and Granados et al. (2016). However, this pattern may have been caused by combining stations harvested using different techniques at different time intervals (six to eight years after RIL and twenty years after CL) as "logged", and similarly, combining undisturbed forests and regenerating shifting agriculture as "unlogged". Further, logging has been reported to negatively impact population densities of small carnivores in Borneo (civets, Heydon and Bulloh, 1996), but such effects may be missed when investigating occupancy. As disturbance, partly derived from logging, impacted occupancy of some carnivores in the FMU, further studies in more homogenous logged areas are needed to assess the susceptibility of sensitive carnivores and potential of recovery after logging.

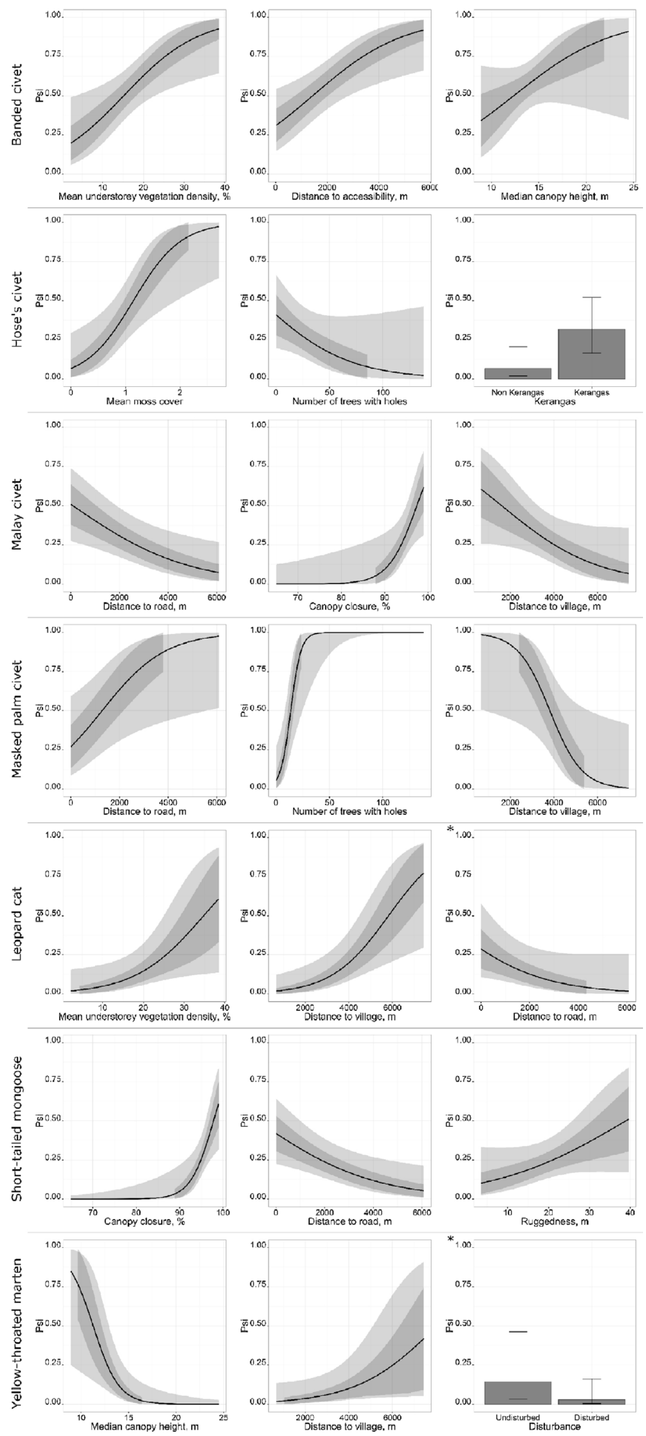

Fig. 2. Response curves of habitat associations for the seven carnivore species for which occupancy models were built. Curves were based on the top model in Table 4. Dark gray shows standard errors and lighter gray represents 95% confidence intervals (CIs). For categorical variables, only 95% CIs are shown.
*Indicates response curve for corresponding variable from the second best model for that species (see Table 4).

Distance to accessibility affected only banded civet: occupancy was higher in less accessible areas, i.e. areas expected to have fewer hunters. However, logging roads (one of the covariates from which d_access was derived) had a more diverse impact on carnivore occupancy. Occupancy of Hose's civet and masked palm civet were lower at stations closer to roads, but our data did not allow us to tease apart a preference for remote forests and increased hunting pressure facilitated by logging roads (Brodie et al., 2015b; Granados et al., 2016). Interviews (unpublished data) showed that banded civet, and particularly Malay civet and masked palm civet, are opportunistically hunted and consumed in the FMU. Further, snares, traps and nets are used that catch animals indiscriminately, possibly affecting the more ground-dwelling carnivores such as banded civet, Malay civet, masked palm civet and Hose's civet. Occupancy of Malay civet, short-tailed mongoose and leopard cat, however, were higher at stations closer to roads, suggesting that logging roads may ease movement, dispersal and/or hunting for these species (see below).

Apart from these species-specific responses linked to the two main threats of logging (via forest disturbance) and human access, our analyses have helped fill knowledge gaps in our understanding of habitat associations for the following species.

Banded civet

Banded civet occupancy was higher at less accessible stations with higher canopies and denser understory vegetation (Table 4, Fig. 2). The relationship with understory vegetation may reflect the feeding behaviour of this species whose diet consists largely of insects (Davis, 1962), and to a lesser degree, earthworms and other small animals (Ross et al., 2015). Understory vegetation not only provides a more heterogeneous microhabitat for a wide variety of prey, but also offers cover to hunt and subsequently consume prey without being disturbed. Trees with higher canopies are associated with lower- to mid-elevations, suggesting this species may not be so common in the upper elevation forests. Further, the sister species of the banded civet, Hose's civet, had higher occupancy in the mid- to higher-elevation forest, which might indicate intraspecific competition between the two species in this FMU. These results are similar to that of Jennings et al. (2013) who suggest banded civet is mainly found in lowland areas whereas Hose's civet primarily occurs at higher elevations, though there may be some overlap among the two at mid-elevations. To test this hypothesis, additional data would be needed, allowing a two-species occupancy analysis.

Hose's civet

Hose's civet occupancy was greater at stations in kerangas forest and where moss cover was high (Table 4, Fig. 2). Because kerangas forests are generally low in mammalian diversity and abundance, species selecting kerangas forest are thought to be specialised (Brunig, 1974). Moss cover was high in areas that have constant high humidity, such as closed canopy, undisturbed forests. Our analysis showed that occupancy of Hose's civet may also be greater in undisturbed stations with high canopy closure, more distant from roads, and in areas with a topography of dips and small valleys. Leaves may accumulate in such dips and small valleys, providing more suitable conditions for earthworms, frogs and other invertebrates, which comprise most of the species diet, as stated by personal communications with indigenous people during the surveys. The relationship of occupancy with low number of trees with cavities may either indicate that tree cavities are not limiting for this species or it may be a spurious relationship.

Malay civet

Malay civet occupancy was higher at stations closer to roads and with higher canopy closure (Table 4, Fig. 2). This is not surprising as this species appears to be one of the more tolerant and adaptable of Bornean carnivores (Ross et al., 2016; Mathai et al., 2016a) and may use logging roads to move or hunt. Occupancy was greater at stations closer to villages, possibly explaining why Malay civet is one of the more common carnivores consumed by local communities in the FMU, and could support earlier accounts that suggest this species scavenges food in settlements (Jennings et al., 2010a; Duckworth et al., 2016a). Although found more frequently closer to roads (and villages), Malay civets require forest cover, for example, for rest sites, which are often associated with high canopy cover (Colon 2002; Jennings et al., 2006). In our study site, this did not restrict the species to less disturbed forests as in situ habitat surveys showed that canopy cover can be high in less disturbed and disturbed forest alike. This result corroborates earlier studies in monoculture plantations in Sarawak (Giman et al., 2007), Peninsular Malaysia (Jennings et al., 2010a) and Sumatra (Jennings et al., 2015) which showed this species did not venture far into plantations from surrounding forests and that dense cover and forested patches were important for this species to survive in such modified habitats.

Masked palm civet

Although one of the more widespread civets in Asia, surprisingly little is known about masked palm civet habitat use across much of its range (Belden et al., 2014). Whereas in central south-eastern China it has been reported to use farmland-dominated landscapes with remnant forest fragments (e.g. Wang and Fuller, 2003; Zhou et al., 2008), there seem to be no records far from forest within the southern part of its range (Duckworth et al., 2016b). It appears to occur mainly at higher elevations with few records from lowland areas anywhere in its Southeast Asian range (Belden et al., 2014). This species was detected mainly at higher elevations in the FMU, with greater occupancy at stations more distant from logging roads, though closer to villages, and where the number of trees with cavities was high. This species may avoid roads due to the access provided to hunters; though not perceived as a scavenger or poultry raider like the Malay civet, it is similarly hunted opportunistically. With fruit making up a large portion of its diet (Duckworth et al., 2016b; Semiadi et al., 2016), masked palm civet frequent areas closer to villages to feed in orchards and fruit gardens of local communities. The association with higher number of trees with cavities may be an indication of use as denning sites.

Leopard cat

Leopard cat is the most widespread Asian cat species. Recent genetic analysis suggests species-level distinctions between the Indochinese and Sundaic populations (Luo et al., 2014), with several of the recognised subspecies exhibiting distinct morphological differences (Sicuro and Oliveira, 2015). At least some of these subspecies or populations exhibit different ecological characteristics, which in turn influence the degree to which they are impacted by various threats and thus, require conservation interventions (Izawa et al., 2009). In our study, leopard cat occupancy was higher in stations with denser understorey vegetation and further from villages. Similar to the banded civet, the dependence on understorey vegetation may reflect its entirely carnivorous diet consisting mainly of small mammals, as well as reptiles, amphibians, birds and insects (Rajaratnam et al., 2007). These prey types may be more abundant within the understorey vegetation of forests. That leopard cats prefer less disturbed forests and have higher occupancy away from villages is surprising as earlier studies of leopard cats in the tropics showed the species occurring in plantations such as acacia (Giman et al., 2007), oil palm (Rajaratnam et al., 2007) and sugar cane (Lorica and Heaney, 2013), having higher densities in more disturbed forests and generally preferring more open forests (Mohamed et al., 2013). Our finding that leopard cats prefer to be closer to logging roads (Fig. 2), however, supports earlier studies showing that leopard cats travel on logging roads and likely use them when hunting (Mohamed et al., 2013).

Short-tailed mongoose

Similar to Malay civet, occupancy of short-tailed mongoose was higher at stations closer to logging roads and with higher canopy closure. Roads possibly enhance movement for this species though the cover of forest is still required. Although many of our records were from more disturbed habitat in the FMU, there is yet no evidence of extensive use of modified habitat, such as monoculture plantations on Borneo, though this species has been recorded close to plantation-forest boundary (Giman et al., 2007; Joanna Ross, personal communication). This species is thought to occur mainly at elevations between 0 and 600 m (Jennings and Veron, 2011) and was recorded only at low elevations (<160 m) in Peninsular Malaysia (Jennings et al., 2010b), whereas our records (though mainly from lower to mid elevations of 250–900 m), ranged up to 1300 m. This is similar to recent records from the Crocker Range in Sabah at more than 1400 m (Andrew Hearn and Joanna Ross, personal communication), indicating that occurrence at such altitudes is not unusual in Borneo. Interestingly, albeit not significant, our analysis showed this species may prefer rugged areas, possibly along ridges. In the SL FMU these features also occur at lower elevations.

Yellow-throated marten

Occupancy of this species was higher at stations with lower canopy height and further away from villages. Preference for stations further away from villages is supported by Hon et al. (2016), who reviewed most of the occurrence records across Borneo and concluded that this species may not go near human populated areas. This may be due to higher conspicuity (Grassman et al., 2005), leading to higher probability of being hunted. Our data further suggests this species is restricted to mid to higher elevation forests of the PZ, which supports the recommendation of Hon et al. (2016) for additional surveys in high-elevation forest to better understand yellow-throated marten habitat use.

Conclusion

Knowledge about fine-scale habitat associations of species and their responses to anthropogenic influences is critical for species conservation in rapidly-changing environments. Our findings show that when left to regenerate, logged forests can provide valuable habitat for many carnivore species, as long as less disturbed habitats are available nearby. Broad management recommendations include: maintaining forest cover adjacent to logging roads, both in flat and rugged areas; preserving blocks of less-accessible, mid- to high-elevation forest with understorey vegetation; and preserving fruiting trees and trees with cavities, both standing and fallen. Our results also highlight the need to consider often overlooked habitat variables, for example, moss cover and kerangas were the most important variables for the little-known Hose's civet and the maintenance of such forest types may be important for species persistence. We were unable to investigate the direct effects of hunting and instead used proxies such as distance to roads or accessibility. However, in discussions with local communities, we learned that hunting levels are increasing, particularly due to ease of access provided by roads to outsiders and the increased use of indiscriminate hunting methods such as snares and nets. Thus, quantifying hunting and its effects on carnivore populations is an important next step for future research not only in this FMU but across Sarawak and Borneo.

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Appendix Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2017.04.002.

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