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Original paper

Terrestrial mammal species richness and composition in three small forest patches within an oil palm landscape in Sabah, Malaysian Borneo

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Abstract. Small and highly degraded forest patches are usually scattered across oil palm plantation landscapes and often exist as permanent features. By using a combination of camera-trapping and line-transect methods, we evaluated the usefulness of three such forest patches (< 30 ha) for terrestrial mammal species conservation in a mature oil palm plantation located near (< 1.7 km) a large continuous tract of logged forest in eastern Sabah, Malaysian Borneo. Of the 29 terrestrial mammal species recorded in this study, 28 were found in the continuous logged forest habitat including six species that are either large-bodied, wide ranging, locally rare or are of high conservation concern. In comparison, 18 species were recorded across the three forest patches collectively; consisting mostly of species that are widespread, well-adapted to living in highly modified habitats and of low conservation concern. The presence of small forest patches within the oil palm habitat matrix seemed to be useful to some extent for some mammal species. However, many of the species were likely only transient in this habitat. The maintenance of large continuous tracts of natural forest is critical to the continued survival of many terrestrial mammal species on Borneo, particularly for species that are of high conservation value.

Key words: camera trapping, fragmentation, mammals, oil palm plantation, Sabah Borneo.

The conversion of lowland tropical rainforests to large-scale plantations of oil palm across the tropics, particularly in Southeast Asia, has led to the significant loss and fragmentation of once large and continuous rainforest habitats (Sodhi et al. 2004; Koh and Wilcove 2009). This has led to significant changes in terms of species composition and relative abundance of the different biological communities inhabiting them (Fitzherbert et al. 2008; Koh and Wilcove 2008; Foster et al. 2011). Intact forests are undoubtedly important and irreplaceable for sustaining tropical biodiversity (Gibson et al. 2011), but despite the high level of degradation in logged-over forests, these forests have often been found to retain considerable conservation value to overall biodiversity, as well as species of high conservation concern (Berry et al. 2010; Edwards et al. 2011; Woodcock et al. 2011; Payne and Davies 2013; Struebig et al. 2013). Yet, many logged forests, particularly those that are highly degraded, are subject to ongoing pressure for conversion to agriculture, mainly oil palm in Southeast Asia (McMorrow and Talip 2001; Fitzherbert et al. 2008; Koh and Wilcove 2008).

The clearing of forests for new oil palm plantations usually results in many small, highly degraded forest patches. Despite the degradation, these isolated forest patches often become a permanent feature of the agricultural landscape. The retaining of such forest patches in oil palm estates, particularly those that have High Conservation Value (HCV), has been promoted by the Roundtable on Sustainable Palm Oil (RSPO) certification program as a means of mitigating biodiversity loss within and around oil palm plantations (Yaap et al. 2010). Although its overall effectiveness has not been widely demonstrated, strategies such as this are generally perceived as useful practices for enhancing biodiversity and are thus forming part

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of a ‘wildlife-friendly’ management system in oil palm plantations (RSPO 2013).

Only few studies have specifically examined the value of forest patches within oil palm habitat matrix for vertebrate conservation. Vertebrate species that are capable of flight, such as birds and bats, are known to benefit to a certain extent from the presence of forest fragments, particularly larger ones (> 300 ha) within converted habitat matrix (Peh et al. 2006; Struebig et al. 2008). For example, it has been suggested that the value of agricultural plantations for bird conservation could be increased by retaining forest patches within or nearby plantations (Peh et al. 2006; Koh 2008; Azhar et al. 2011), though results have not always been consistent (e.g., in < 90 ha fragments, Edwards et al. 2010). To the best of our knowledge, only two studies have examined the value of forest patches within or adjacent to oil palm plantations for terrestrial mammal species conservation (i.e., Numata et al. 2005; Azhar et al. 2014); both were conducted in Peninsular Malaysia and both studies revealed lower mammal species diversity in forest patches. No studies on terrestrial mammals in forest patches within oil palm plantations have ever been conducted in the Malaysian state of Sabah on northern Borneo, despite the fact that more than 1.2 million hectares or 16% of the state’s land area had been planted with oil palm (McMorrow and Talip 2001; Brühl and Eltz 2010). Ultimately, the conservation value of retaining small forest patches inside oil palm plantations is still poorly known for terrestrial mammals.

By using a combination of camera-trapping techniques and line-transect method, we carried out the present study to assess the value of retaining small and highly degraded forest patches within a mature oil palm plantation for terrestrial mammal species conservation. Our study primarily assessed species richness and community composition of medium- to large-sized terrestrial mammals utilising the forest patches in the oil palm plantation. In addition, we also assessed the effects of forest patch size and isolation, as well as their quality in terms of habitat structure, on the richness of these mammal communities.

Methods

Study area

This study was conducted in Tabin Wildlife Reserve (5°10'–5°15'N, 118°30'–118°45'E) and in three adjacent forest patches located in an oil palm estate, all in the east of Sabah, Malaysia on northern Borneo (Fig. 1). More than 95% of Tabin Wildlife Reserve (120,521 ha in area) has been selectively logged from the early 1960s until 1989 (Sale 1994). Tabin was gazetted as a wildlife reserve in 1984 primarily to serve as a refuge site for animals displaced by the logging activities and extensive agricultural development in the region (Sale 1994). The four largest land mammals on Borneo are reported from the reserve, all of which are among the most globally threatened: Sumatran rhinoceros, *Dicerorhinus sumatrensis*, Bornean pygmy elephant, *Elephas maximus borneensis*, Bornean orangutan, *Pongo pygmaeus morio*, and Banteng, *Bos javanicus* (Sale 1994; IUCN 2013).

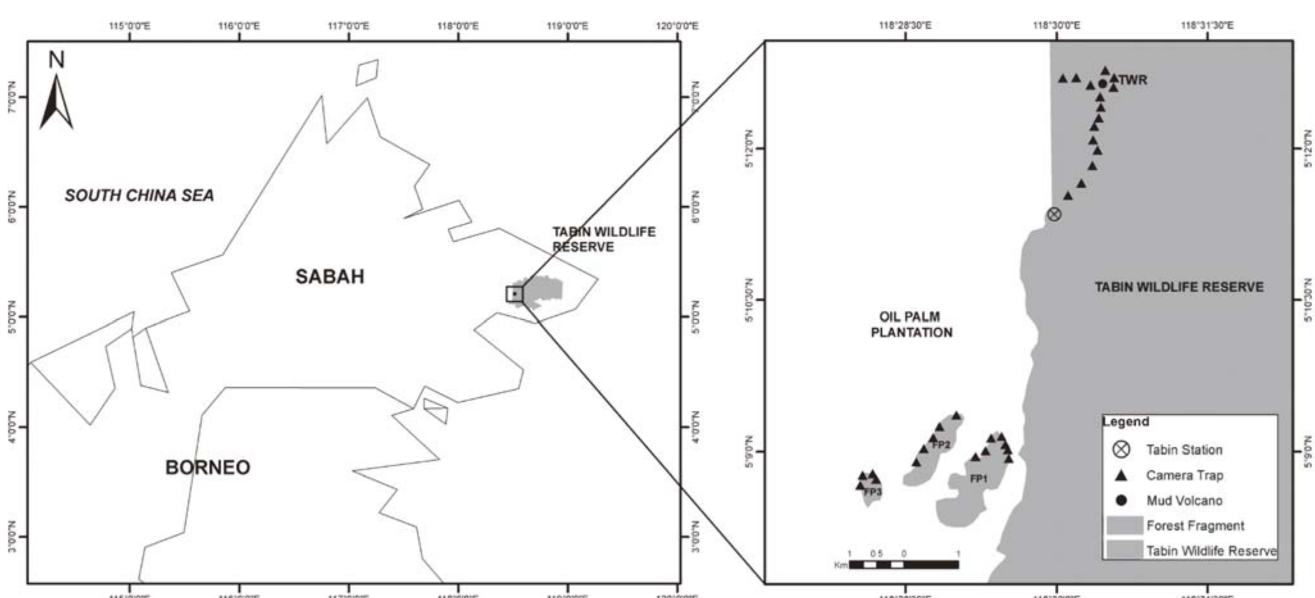

Fig. 1. Map of the study area at Tabin Wildlife Reserve, in the east of Sabah, Malaysia, northern Borneo, indicating the camera-trapping sampling sites.

The vegetation of Tabin comprises mixed lowland dipterocarp rainforest with floral composition typical of the lowland forests across much of northern Borneo (Mitchell 1994). The land surrounding Tabin has been progressively converted to agricultural plantations over the past five decades. Initially this region was planted with cocoa and rubber trees (Sale 1994), but in later years and at the present time, these were supplanted by oil palm as the dominant crop. Today Tabin forest is completely isolated, surrounded by large-scale plantations of oil palm which range in age from very recent plantings, to stands more than 25 years old. Older plantations are continuously replanted with new palms.

Small forest patches, ranging in size from 0.5 to 30 ha, occur amidst the plantation landscape. These forest fragments, many of which are located on hilly areas, were initially cleared of all vegetation during the plantation's development. However, steeper areas usually have a lower oil palm yield owing to the presence of many huge boulders and steep rock walls. These conditions have rendered the planting of oil palm to be not cost-effective at such places, and hence, they were never planted. With time, these cleared areas were recolonised by secondary vegetation to form forest patches that are found today.

Study design

Ideally, we would have included many forest patches in our study, but logistical difficulties prevented us from doing so. We therefore focus our appraisal at the scale of a typical oil palm plantation, and the number of forest patches typically available for conservation by estate management. Specifically, we investigate the habitat value for mammals of three forest patches (or FP) of small sizes: FP1 (27 ha), FP2 (16 ha), and FP3 (5 ha) (Fig. 1). These patches were located in a mature oil palm estate (5,210 ha) with palm trees of > 20 years old (ca. 10–20 m tall) and occurring at a density of ca. 100 palms/ha near to the western border of Tabin. Sampling sites ranged in distance from 0.5 km, 1.1 km and 1.7 km from FP1, FP2 and FP3 to the western border of Tabin, respectively. The forest patches were separated from each other by distances of 0.6–1.6 km within the matrix habitat of oil palm. Distance measurements were estimated using a GPS unit. It is likely that forest patches have been isolated from the Tabin forest for at least 25 years, when the plantation was established around 1986 (Nomura et al. 2004). To serve as a control, one sampling site (TWR) representing larger, continuous forest habitat was selected from within Tabin for comparison. This last site was located in the western part of the reserve, approximately 0.7 km deep inside forest that was logged at least twice in the 1980s (Mitchell 1994). Due to the proximity of forest patches to the western border of the reserve and the common forest type, topography and elevations they shared (100–300 m a.s.l), we assumed that prior to the establishment of the plantation, all sampling sites had similar mammalian communities. To obtain information on mammal species richness and community composition, two survey methods were employed; (1) camera-trapping, and (2) line-transect methods.

Camera-trapping

Camera-trapping was conducted using automatic, motion-triggered, digital camera traps (Cuddebacks-Capture, Non Typical, Inc. USA). Since the number of camera traps was limited, camera-trapping was carried out at the sampling sites in TWR and the FP sites in two alternating sessions of four months each as follows: TWR (May to August 2009 and January to April 2010); FP1, FP2 and FP3 (September to December 2009 and May to August 2010). At TWR, 15 camera stations each consisting of a single camera trap were established located at every 200 m intervals along an existing 2.7 km human-made trail inside the forest. Since the forest patches in the oil palm plantation were unequal in size, and much smaller than Tabin, fewer single camera trap stations were necessarily established at the FP sites: 7, 5 and 4 locations in FP1, FP2 and FP3, respectively. Camera stations in the FP sites were established 30–50 m from forest patch edges along a newly cut trail running parallel to the forest patch edges. Distances between camera trap stations in the FP sites were 50–100 m. All stations at all sites were placed in relatively open habitat (i.e., along trails), to minimise inter-site variation in detection probability of species caused by differing use of habitats according to varying vegetation density at ground level (< 2 m). Moreover, forest trails are generally known to be travelled frequently by many mammal species (Bernard et al. 2013; Mohamed 2013; Mohamed et al. 2013). Placing camera stations along forest trails therefore maximises the potential of photo-capture of as many terrestrial animal species as possible. All camera traps were attached to the base of trees approximately 30–50 cm from the ground and each was programmed to take one photograph at every triggering event, with a minimum 60 second interval between successive triggers. All camera traps were active 24h per day and used white flash at night. No baits or lures were used near or around camera traps during the course of the study.

Line-transect

The line-transect method was employed to supplement data obtained from the camera-trapping. This method involved two observers walking silently at a constant speed of about 0.5–0.8 km/hour along non-random line-transects located on the same trails where camera-trap stations were fixed. Transects lengths varied from the longest at 1.9 km (at TWR), to 0.8 km (FP1), 0.6 km (FP2) and 0.4 km (FP3) among the forest patches. In addition, efforts were made to survey other areas within a 50 m radius of camera trap stations. During walks, frequent but brief stops were made at every 20–30 m distance, to allow careful searching for animals at all heights in the forest from ground level, to the middle and upper canopy layers. All mammal searches were aided by a pair of binoculars and head-torches when necessary and conducted during fine weather in early morning from 0545 hours to 1030 hours. Records of animal presence were also made via indirect sign of animal activities, such as calls or vocalisation, nests, tracks, and claw marks on tree trunks. Only fresh animal signs (< 1 day old) were considered, and only when the species identity was known with high certainty was it recorded. Identification of animals directly observed or via their signs was based on descriptions from Payne et al. (1985) and the past experience of the observers. Nomenclature followed Wilson and Reeder (2005). An observation of animal sign could indicate the presence of either one individual, or a group of animals. To standardise abundance data recording conservatively, all indirect observations made of a species were regarded as being made by only one animal. All trails at all sampling sites were walked at least three consecutive days per month over a total 12 month period (May 2009 to April 2010). To control for sampling bias due to variation in observer efficiency, the same observers (ELB and research assistant) recorded all observations throughout the study.

Vegetation structure

To quantify the vegetation structure and its impact on mammal presence-absence, we recorded the following 11 variables: (1) % cover of leaf litter, (2) % cover of ground vegetation (≤ 2 m above ground), (3) % cover of low vegetation (2 to 5 m above ground), (4) % cover of understory vegetation (5 to 20 m above ground), (5) % cover of canopy layer (≥ 20 m above ground), (6) height of canopy (m) and number of trees with the following diameter classes (dbh): (7) 10–20 cm, (8) > 20–30 cm, (9) > 30–40 cm, (10) > 40–50 cm, and (11) > 50 cm. All variables were recorded via visual estimation by the same observer (ELB) within a circular plot (5 m radius) from areas adjacent to (ca 15 m), but not at or surrounding, camera-trap stations or trails.

Data analysis

Photographs of mammals captured from the camera traps were identified as much as possible to species level based on Payne et al. (1985) and expert knowledge of the authors. Nomenclature followed Wilson and Reeder (2005). Photographs of rats and bats were, however, excluded from the analysis, as the individual animals in those photographs were too small to make positive species identification. Additionally, as some congeneric species were on occasion hard to distinguish from the photographs, for example muntjacs, mouse deer, mongooses and treeshrews; these were all pooled into their respective genera.

To reduce temporal autocorrelation of photo-capture events, multiple photos of the same species recorded from the same camera-trap station < 1 hour apart were treated as a single record. Exceptions to this included clear instances where consecutive photographs clearly depict different individuals such as can be identified by physical body condition, age and/or sex of the animal, or some other distinctive physical characteristics. Overall camera trap detection rates were determined for all animal species combined, and also for each individual species, for each sampling site. Trap detection rates (D) for each species were calculated as the number of independent photographs captured of a species (C) per 100 trap-nights using the formula: $D = C \times 100/\Sigma N$, where ΣN is the total number of camera trap-nights accumulated during the study, accounting for camera loss (due to theft or vandalism) and/or malfunctions. In this study, detection rates were used as an index of relative abundance. Although the constraints associated with using indices have received much attention (e.g., Jennelle et al. 2002; Sollmann et al. 2013), they have received some validation in the context of camera trap studies (e.g., Carbone et al. 2001, 2002; O'Brien et al. 2003; Rovero et al. 2005; Jenks et al. 2011).

In order to compare the observed species richness across sites, we used abundance-based rarefaction curves with 95% CI. The species richness accumulation curves were constructed in EstimateS (Version 9.1.0, Colwell 2013) based on 100 random iterations. We used cumulative number of camera trap-nights in each site as a standardised measure of sampling effort. We also estimated the asymptotic mammal species richness for each of the sampling sites, using five commonly used non-parametric species richness estimators calculated using EstimateS: Chao1, Jacknife1, ICE (incidence-based coverage estimator), ACE (abundance-based coverage estimator) and Bootstrap methods (Colwell and Coddington 1994).

To assess the sampling completeness of the mammal communities at each site conservatively, we calculated the observed species number as a proportion of the estimated species richness, derived as the mean of the five selected non-parametric species richness estimators. Sampling was assumed to be sufficient when this proportion approached unity. To compare the similarity of mammal species composition between sites, we calculated the Sørenson similarity coefficient (Sørenson 1948). Pooled data from both species presence-absence records (i.e., data from both camera-trapping and line-transect methods) were used for our analyses.

We used multivariate Principal Component Analysis (PCA) to analyse the vegetation structure of the sampling sites. PCA was used to reduce the large number of variables to a smaller set of principal components (PC) that effectively summarises only essential information contained in the variables. Only PC's with eigenvalues of > 1.0 were extracted in the analysis. Prior to running analyses, all variables were transformed in order to satisfy the normality assumption of PCA. Arc-sine transformation was used for all variables measured as percentages, and square root transformation was used for all count variables. To investigate the relationship between mammal species richness and habitat structure, the extracted PCs and observed species richness were used to calculate Pearson's r correlation (Zar 1999). All analyses were performed using Statistical Package for the Social Sciences version 20.0 (SPSS Ins., Chicago, IL) and we used a standard threshold significance value of $P \leq 0.05$.

Results

Mammal species richness and abundance

We accumulated a total camera-trapping effort of 3,733 camera trap-nights and recorded 2,145 photographs of mammals; of these, 1,871 (or 87% of the total photographs captured) were independent photographic events (Table 1). A total of 26 mammal species representing 16 taxonomic families and seven orders were recorded. For the line-transect method, we accumulated a total sampling effort of 288 hours of field observations. These resulted in 77 independent detections of animals and their signs from 18 mammal species representing 15 taxonomic families and six orders (Table 2). The two survey methods combined recorded a total of 29 terrestrial mammal species; 28 species in TWR and 18 species from the three FP sites collectively.

Based on the camera-trapping records, the observed species richness and relative abundance of all species combined were two- to three-folds higher in TWR than in the three forest patches (Table 1). The pattern of the observed species richness across all four sites was also in agreement with the five commonly used abundance-based estimators of species richness (Fig. 2). However, the species accumulation curves revealed a more complicated picture. Specifically, at low sampling effort the species detection rates were higher for all forest patches than for TWR (Fig. 3). But, at higher sampling effort, TWR exhibited a higher species detection rate. When compared to pooled camera-trapping data across all FP sites, the species detection rate was significantly higher for TWR at around ≥ 500 camera trap-nights.

The sampling completeness indices calculated for each site were reasonably high, with values ranging from 0.81 to 0.96 (TWR = 0.96; FP1 = 0.81; FP2 = 0.88; FP3 = 0.89). This suggests that the sampling saturation for the camera-trapping method was relatively high at all sites. Results from the line-transects were generally comparable to that obtained via camera-trapping with respect to species richness and relative abundance across all sampling sites, though the sample size for this survey method was low (Table 2).

Species composition

Based on pooled data of species presence-absence from both camera-trapping and line-transect, the largest forest patch (FP1) was more similar to TWR (Sørensen index = 42%) in terms of species composition than either of the others. We determined that FP3 is more similar to both FP1 (39%) and FP2 (38%), and the lowest similarity existed between FP1 and FP2 (30%). Overall, the four sampling sites appeared to indicate a nested subset pattern of species composition (Table 3). Thus, species encountered in the smallest forest patches (FP2 and FP3) generally tended to also occur in both the largest forest patch (FP1), and in the continuous forest of Tabin (TWR). However, some species recorded from the larger forest patch, and many species recorded from the continuous forest, were altogether absent from the smallest forest patches.

Table 1. Mammal species relative abundance based on camera-trapping records

ORDER/Family	Scientific name	Common name	Photographic rate per 100 camera trap-night				
			TWR	FP1	FP2	FP3	Total
CETARTIODACTYLA							
Cervidae	*Muntiacus* spp.	Muntjac spp.	5.89	0.21	0	1.31	4.37
	Rusa unicolor	Sambar deer	2.81	0	0	0	2.04
Bovidae	*Bos javanicus*	Banteng	0.04	0	0	0	0.03
Suidae	*Sus barbatus*	Bearded pig	20.37	5.34	1.30	0.87	15.59
Tragulidae	*Tragulus* spp.	Mouse deer spp.	7.30	0	0	0	5.28
CARNIVORA							
Felidae	*Neofelis diardi*	Clouded leopard	0.19	0	0	0	0.13
	Pardofelis badia	Bay cat	0.07	0	0	0	0.05
	Prionailurus bengalensis	Leopard cat	0.26	2.01	0.98	0.87	0.59
	Pardofelis marmorata	Marbled cat	0.07	0	0	0	0.05
Mustelidae	*Martes flavigula*	Yellow-throated marten	0.04	0	0	0	0.03
	Mustela nudipes	Malay weasel	0	0.21	0	0	0.03
Mephitidae	*Mydaus javanensis*	Sunda stink-badger	0	0	0.65	0.44	0.08
Ursidae	*Helarctos malayanus*	Sun bear	0.74	1.85	0	0	0.78
Viverridae	*Hemigalus derbyanus*	Banded palm civet	2.26	1.03	0.33	0.87	1.85
	Viverra tangalunga	Malay civet	1.30	1.85	0	0.87	1.23
	Paradoxurus hermaphroditus	Common palm civet	0.52	0	0.65	0	0.42
Herpestidae	*Herpestes* spp.	Mongoose spp.	0.30	0.41	0	0	0.27
EULIPOTYPHLA							
Erinaceidae	*Echinosorex gymnura*	Moonrat	1.07	0	0	0	0.78
PRIMATES							
Cercopithecidae	*Macaca fascicularis*	Long-tailed macaque	0.07	0	0	0	0.05
	Macaca nemestrina	Pig-tailed macaque	13.74	11.29	9.77	10.92	12.89
Hominidae	*Pongo pygmaeus morio*	Bornean orangutan	0.07	0	0	0	0.05
PROBOSCIDEA							
Elephantidae	*Elephas maximus borneensis*	Bornean elephant	0.59	0	0	0	0.43
RODENTIA							
Hystricidae	*Hystrix brachyura*	Common porcupine	1.59	2.46	0.65	0	1.53
	Hystrix crassispinis	Thick-spined porcupine	0.93	0.21	0	0	0.70
	Trichys fasciculata	Long-tailed porcupine	0.07	0.21	0	0	0.08
SCANDENTIA							
Tupaiidae	*Tupaia* spp.	Treeshrew spp.	0.19	4.52	0	1.31	0.80
	Overall photographic rate	100 camera trap-nights	60.89	31.99	19.87	21.83	50.12
		Total indep. photographs	1,633	154	44	40	1,871
		Total camera trap-nights	2,700	497	307	229	3,733
		Total number of species	24	13	7	8	26

Many of the species we detected at our sites were classified as threatened in some way based on the IUCN (2013) criteria. Four species encountered in the continuous forest (TWR) are regarded as “Endangered”, eight “Vulnerable” and one “Near Threatened” species (Table 3). All combined however, forest patches contained only four “Vulnerable,” one “Near Threatened,” and no “Endangered” species. All of the other species recorded in forest patches are currently classified as either “Least Concern” or “Data Deficient”. When only the smallest forest patches were considered (FP2 and FP3), the number of “Vulnerable” species recorded was even smaller (3 species), while the remaining species (8 species) in these sites are classified as either “Least Concern” or “Data Deficient”.

Table 2. Mammal species recorded based on line-transect method

ORDER/Family	Scientific name	Common name	Number of individuals detected				
			TWR	FP1	FP2	FP3	Total
CETARTIODACTYLA							
Cervidae	*Muntiacus* spp.	Muntjac spp.	2	0	0	0	2
	Rusa unicolour	Sambar deer	3	0	0	0	3
Suidae	*Sus barbatus*	Beaded pig	8	1	0	1	10
Tragulidae	*Tragulus* sp.	Mouse deer sp.	6	0	0	0	6
CARNIVORA							
Felidae	*Prionailurus bengalensis*	Leopard cat	0	1	0	0	1
Mustelidae	*Martes flavigula*	Yellow-throated marten	0	2	0	0	2
	Mustela nudipes	Malay weasel	1	2	0	1	4
Ursidae	*Helartos malayanus*	Sun bear	1	0	0	0	1
Viverridae	*Paradoxurus hermaphrodites*	Common palm civet	1	0	0	0	1
Herpestidae	*Herpestes* spp.	Mongoose spp.	1	3	0	0	4
PRIMATES							
Cercopithecidae	*Macaca fascicularis*	Long-tailed macaque	2	0	0	0	2
	Macaca nemesterina	Pig-tailed macaque	10	11	4	2	27
Hominidae	*Pongo pygmaeus morio*	Bornean orangutan	1	0	0	0	1
Hylobatidae	*Hylobates muelleri*	Bornean gibbon	1	0	0	0	1
PROBOSCIDEA							
Elephantidae	*Elephas maximus borneensis*	Bornean elephant	2	0	0	0	2
RODENTIA							
Hystricidae	*Hystrix brachyuran*	Common porcupine	0	1	0	0	1
Sciuridae	*Callosciurus prevostii*	Prevost's squirrel	1	1	0	0	2
	Ratufa affinis	Giant squirrel	1	1	0	0	2
SCANDENTIA							
Tupaiidae	*Tupaia* spp.	Treeshrew spp.	5	0	0	0	5
		Total	46	23	4	4	77
		Sampling effort (hrs)	144	72	36	36	288
		Total number of species	16	9	1	3	18

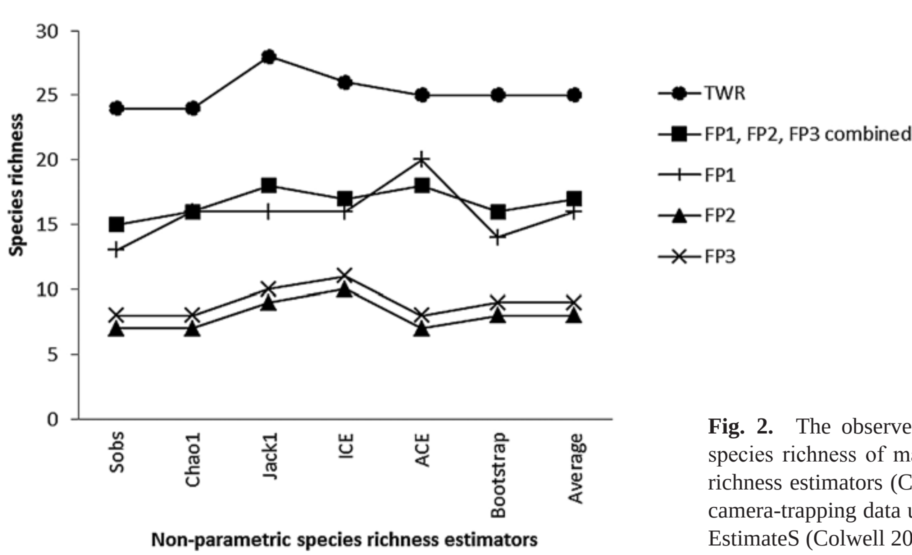

Fig. 2. The observed species richness (Sobs), and the estimated species richness of mammals based on five non-parametric species richness estimators (Chao 1, Jack 1, ICE, ACE and Bootstrap) from camera-trapping data using abundance-based rarefaction approach in EstimateS (Colwell 2013).

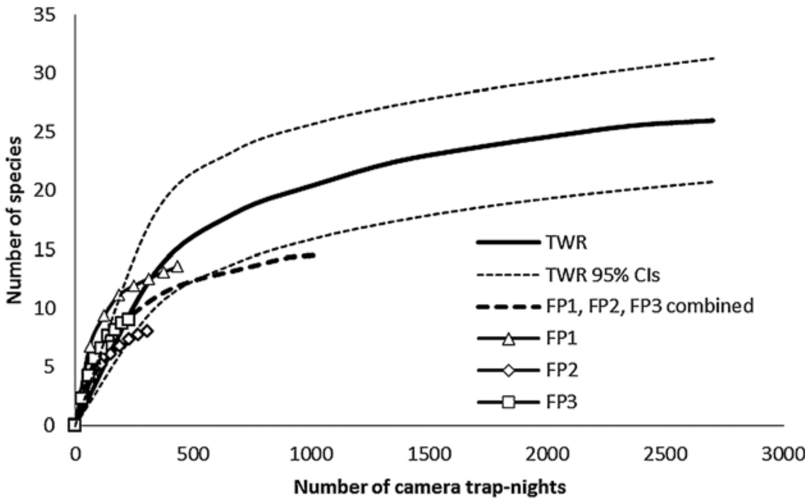

Fig. 3. Observed species richness accumulation curves constructed using EstimateS (Colwell 2013) with cumulative number of camera trap-nights as a standardised measure of sampling effort.

Table 3. Incidence of mammal species at each site based on combined data from camera-trapping and line-transects

Species		Sampling sites				*Number of Sites/IUCN
Scientific name	Common name	TWR	FP1	FP2	FP3	
Hemigalus derbyanus	Banded palm civet	+	+	+	+	4 VU
Sus barbatus	Bearded pig	+	+	+	+	4 VU
Prionailurus bengalensis	Leopard cat	+	+	+	+	4 LC
Macaca nemestrina	Pig-tailed macaque	+	+	+	+	4 VU
Hystrix brachyuran	Common porcupine	+	+	+	–	3 LC
Viverra tangalunga	Malay civet	+	+	–	+	3 LC
Mustela nudipes	Malay weasel	+	+	–	+	3 LC
Muntiacus spp.	Muntjac spp. (E)**	+	+	–	+	3 LC
Tupaia spp.	Treeshrew spp. (E)**	+	+	–	+	3 LC/DD
Paradoxurus hermaphroditus	Common palm civet	+	–	+	–	2 LC
Ratufa affinis	Giant squirrel	+	+	–	–	2 NT
Trichys fasciculate	Long-tailed porcupine	+	+	–	–	2 LC
Mydaus javanensis	Sunda stink-badger	–	–	+	+	2 LC
Herpestes spp.	Mongoose spp.	+	+	–	–	2 LC/DD
Callosciurus prevostii	Prevost’s squirrel	+	+	–	–	2 LC
Helarctos malayanus	Sun bear	+	+	–	–	2 VU
Hystrix crassispinis	Thick-spined porcupine (E)	+	+	–	–	2 LC
Martes flavigula	Yellow-throated marten	+	+	–	–	2 LC
Bos javanicus	Banteng	+	–	–	–	2 EN
Pardofelis badia	Bay cat (E)	+	–	–	–	1 VU
Elephas maximus borneensis	Bornean elephant	+	–	–	–	1 EN
Hylobates muelleri	Bornean gibbon (E)	+	–	–	–	1 EN
Neofelis diardi	Sunda clouded leopard	+	–	–	–	1 VU
Macaca fascicularis	Long-tailed macaque	+	–	–	–	1 LC
Pardofelis marmorata	Marbled cat	+	–	–	–	1 VU
Echinosorex gymnura	Moonrat	+	–	–	–	1 LC
Tragulus spp.	Mouse deer spp.	+	–	–	–	1 LC
Pongo pygmaeus morio	Bornean orangutan (E)	+	–	–	–	1 EN
Rusa unicolor	Sambar deer	+	–	–	–	1 VU
	Total (29)	28	16	7	9	

*Species are arranged in decreasing order by number of sites where a species was present and then alphabetically based on common names (following Laidlaw 2000). IUCN refer to the red list of globally threatened species status; EN = endangered, VU = vulnerable, LC = least concern, NT = near threatened, DD = data deficient (IUCN 2013). (E) = denotes Bornean endemic species; (E)** = denotes some species of this genus are Bornean endemic.

Vegetation structure and correlation with species richness

The PCA reduced the 11 habitat structure variables to two principal components (PC1 and PC2) with eigenvalues greater than 1 (PC1 eigenvalue 4.946 and PC2 eigenvalue 1.813). PC1 and PC2 explained 44.96% and 16.48% of the total variance of the variables respectively, resulting in a cumulative proportion explained of 61.44%. PC1 scores increased with increasing % canopy cover, % leaf litter cover, canopy height, count of trees with dbh > 10–20 cm, > 30–40 cm and > 50 cm and decreasing % ground cover vegetation (Table 4). A high score for PC1 thus represented vegetation structure characteristics of natural forest areas (i.e., tall, closed canopy and with many small-, medium- and large-sized trees). PC2 scores increased with increasing % cover of understorey, trees with dbh 20–30 cm and decreasing % cover of low vegetation and % leaf litter cover (Table 4). A high score for PC2 could therefore be considered representative of highly modified habitat (i.e., dense middle storey cover with many smaller sized trees albeit with less ground cover vegetation). By plotting the scores for individual vegetation plots along the axes PC1 and PC2, three clear groups become evident, with TWR (Group 1) representing the most distinct group and the forest patches being more similar to each other (Fig. 4). However, among the three forest patches, FP2 and FP3 (Group 2) were more similar to each other than to FP1 (Group 3). Scores of PC1 were positively correlated with mammal species number across sites (Pearson $r = 0.94$, $n = 120$, $P < 0.001$), indicating that mammal species tended to occur more in habitat resembling undisturbed forest. Scores of PC2 showed no significant correlation with mammal species number across sites over all (Pearson $r = 0.07$, $n = 120$, $P = 0.46$). However, when PC2 scores were evaluated with respect to species numbers from only the FP sites, a significant negative correlation was detected (Pearson $r = –0.786$, $n = 90$, $P < 0.001$), indicating that to some extent disturbed habitat as defined here was more likely to contain fewer mammal species.

Table 4. Principal component weightings of forest structure variables with eigenvalues > 1

Variables	PC1	PC2
% cover of leaf litter	**0.722**	**–0.412**
% cover of ground vegetation	–0.519	–0.223
% cover of low vegetation	0.526	**–0.736**
% cover of understory	0.362	**0.825**
% cover of canopy layer	**0.923**	–0.046
Canopy height (m)	**0.864**	–0.124
No. of trees dbh 10–20 cm	**0.723**	0.120
No. of trees dbh 20–30 cm	0.380	**0.562**
No. of trees dbh 30–40 cm	**0.842**	0.148
No. of trees dbh 40–50 cm	0.595	–0.003
No. of trees dbh > 50 cm	**0.647**	–0.006

Note: Values in bold highlight variables having the largest contributions to PC1 and PC2.

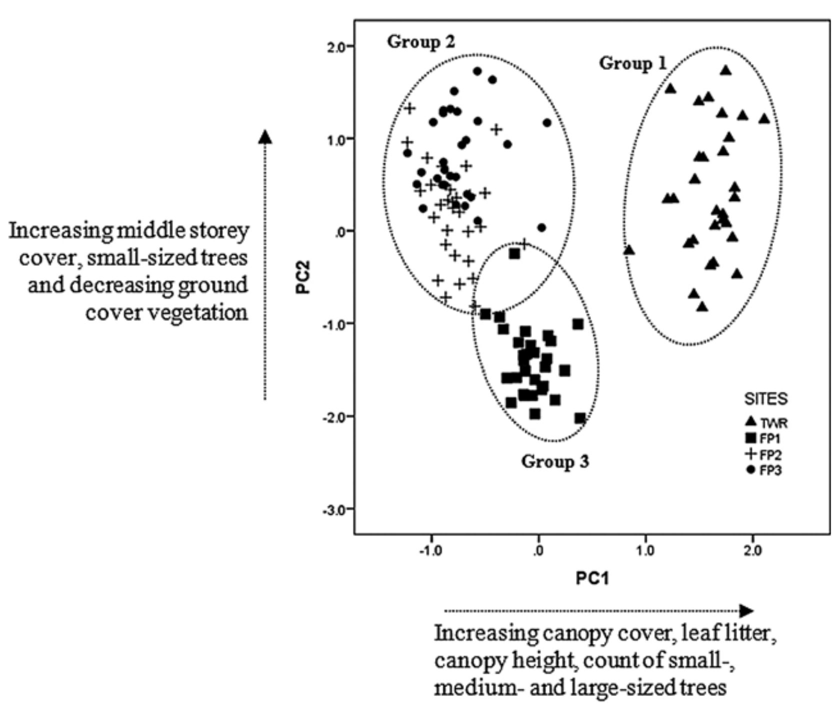

Fig. 4. Two-dimensional scatter diagram of principal component analysis of 11 vegetation structure variables from 120 plots distributed across four sampling sites.

Discussion

Mammal species loss in forest patches

The large continuous forest habitat of Tabin was clearly more species rich than the forest patches within the oil palm plantation. When differences in sampling effort were accounted for, rates of increase in the detection of new species in forest patches were initially higher than in the continuous forest; however, greater sampling effort in the continuous forest showed a much higher species accumulation rate. The difference in patterns of species accumulation rates between the forest patches and continuous forest is likely indicative of forest patches not only having lower species richness overall, but also each species has a lower density. Overall therefore, the diversity of the mammal community in these habitats was relatively lower than in Tabin.

The incidence of species in the sampling sites appeared to follow a nested subset pattern (Patterson 1987), where species that occurred in the smaller forest patch generally also occurred in the larger forest patch, and except for one species (Sunda stink-badger *Mydaus javanensis*) which could have been missed by chance, species that occurred in the larger forest patch were all found in the continuous forest habitat. Species that were regularly recorded in forest patches and that were found across all sampling sites were among those that are most widespread species in Sabah's forests (e.g., banded palm civet, *Hemigalus derbyanus*, pig-tailed macaque, *Macaca nemisterina*, leopard cat, *Prionailurus bengalensis*, bearded pig *Sus barbatus*) (Payne et al. 1985), none of which are of high conservation concern under the IUNC Red List (IUCN 2013). Some of these species are also habitat generalists (e.g., Leopard cat, *P. bengalensis*, bearded pig, *S. barbatus*) and/or group-living animals (e.g., pig-tailed macaque, *M. nemisterina* and bearded pig, *S. barbatus*) (Payne et al. 1985). The most restricted species encountered only in the TWR tended to be either large-bodied animals; including those usually ranging over large areas (e.g., Bornean elephant, *Elephas maximus borneensis*, banteng, *Bos javanicus*, Bornean orang utan, *Pongo pygmaeus morio* and Sunda clouded leopard, *Neofelis diardi*) (Singleton and van Schaik 2001; Alfred et al. 2012; Hearn et al. 2013; Gardner et al. 2014), or species believed to be locally rare (e.g., Felids such as the Sunda clouded leopard, *N. diardi*, bay cat, *Pardofelis badia* and marbled cat, *P. marmorata*) (Wilting et al. 2006; Azlan and Sanderson 2007; Brodie and Giordano 2012). Overall 39% of the mammals recorded in continuous forest were not recorded in the forest patches, including all four species we recorded that are classified as "Endangered" (IUCN 2013).

The extent in species loss in the forest patches as indicated in this study is undoubtedly an underestimation. At least 48 species of terrestrial mammals (excluding volant and non-volant small mammals) have been recorded to be present in Tabin Wildlife Reserve, but many of which were not detected during our study (Bernard and Fjeldså 2003). The sampling methods used to detect mammal species in our study were not suitable for sampling many of the true canopy mammal species, that are mostly nocturnal, and often represent an important component of the tropical rainforest mammal community (Payne et al. 1985). The loss of tall canopy trees in the forest patches can be expected to negatively impact the persistence of true canopy mammals in this habitat.

It is important to note that the number of forest patches considered in this study was low ($n = 3$); variation in forest patch size and distance of the forest patches from the continuous forest were insufficient to make meaningful inferences about the effect of forest area, and isolation of forest patches in oil palm habitat, on mammal species richness. Nevertheless, data from our study indicate that the largest forest patch (27 ha), which was located nearest (ca. 500 m) to the continuous forest, recorded roughly twice as many mammal species than the other two smaller forest patches (16 ha and 5 ha), both of which were also located further away (1,100 m and 1,700 m). The two smaller forest patches, separated by a distance of ca. 600 m from each other, had comparable mammal species number. Despite study limitations in terms of design, our results were consistent with that of Laidlaw (2000), who determined that mammals in a network of small forest areas (70–307 ha) in Peninsular Malaysia conformed to the classic theory of island biogeography (McArthur and Wilson 1967).

Conservation implications

In order for mammal conservation to be most effective in oil palm plantations, results from the present study suggest that more large forest patches are needed amidst the plantation landscape; moreover whenever possible, more patches should be located closer to one or more larger continuous tracts of forest, which could conceivably act as source habitat. Our results also suggest that, although forest patches were relatively close to the Tabin forest, the oil palm plantation is a relatively impermeable habitat to many mammal species particularly species of high conservation value. We did not sample the matrix habitat of oil palm during our study, but extensive camera-trapping within oil palm plantations elsewhere in Sabah as well as in central Kalimantan, Indonesian Borneo, have confirmed a depauperate mammal community inside oil palm plantations (Silmi et al. 2013; Wearn unpublished data). Small mammal (< 1 kg) trapping activities conducted in 2000 in oil palm plantation in the same general areas as the present study are also consistent with these findings (Bernard et al. 2009).

Species occurrence in the forest patches does not necessarily imply permanent residence in the forest patches, or even within the large habitat matrix of oil palm surrounding the forest patches. In this study the proximity of forest patches to continuous forest might have influenced the species number in the forest patches. Studies on Sun bear, *Helarctos malayanus* (Nomura et al. 2004), and common palm civet, *Paradoxurus hermaphorditus* (Nakashima et al. 2013), in Tabin and Malay civet, *Viverra tangalunga* (Jennings et al. 2010), in peninsular Malaysia showed that these species were sometimes found in oil palm plantations, including remnant forest patches within the plantation habitat, but they do not venture very far (ca. 0.6–1.6 km) into the plantation and would often return to the forest. In Tabin, the leopard cat, *P. bengalensis*, is probably one exception to this. Based on our camera-trapping data, the leopard cat was the only species that actually logged higher photographic rates in all the forest patches than in the continuous forest area. Rajaratnam et al. (2007), on the basis of radio-tracking data from six leopard cat individuals in western Tabin, suggested a habitat preference for oil palm in the case of this species, due to a hypothesised higher 'catchability' of murid prey in the oil palm relative to the logged forest. The forest patches were thought to provide cover for resting during the day time inside the plantation, and possibly also for breeding (Rajaratnam et al. 2007). Even so, none of the leopard cat individuals studied by Rajaratnam et al. (2007) used oil palm habitat exclusively and the home ranges of all of the studied individuals encompassed the continuous forest of Tabin to some extent.

Based on the photographic rates recorded in the present study, we suggest that the use of oil palm habitat was similarly transient for many of the species we detected inside forest patches, for example the muntjacs, *Muntjac* sp., bearded pig, *S. barbatus*, banded palm civet, *H. derbyanus*, Malay civet, *Viverra tangalunga* and pig-tailed macaque, *M. nemestrina*. Further studies however are needed for these species and a diversity of other species to determine the relationships more clearly; studies for example including more isolated forest patches within an oil palm matrix and in pure oil palm habitats away from any forest would be particularly useful. To obtain quantitative data on habitat use and demonstrate empirically if these species are either transient or breeding in non-forest habitats, these proposed future studies would have to involve radio-tracking individuals and monitoring how much time they spend in oil palm, forest and other habitats.

Finally, even though our results suggest that patch size and degree of isolation from continuous forest habitat play central roles in determining mammal species richness in remnant forest, there is some evidence from this study for an additional role played by habitat quality. Forest patch size and degree of isolation may interact with aspects of habitat quality, but if the effects of these factors were held constant, our study suggests that the more similar a fragment's habitat structure is to continuous natural forest, the greater the number of mammal species it will likely contain. Hence, in addition to patch size and degree of isolation, the lower richness of terrestrial mammal species recorded in forest patches in our study was possibly due in part to the lower vegetation complexity. This in turn suggests that in order to increase the value of forest patches for mammal conservation in oil palm plantations, habitat quality is one of the key factors that needs to be improved. Taking into account the results of our study, we suggest that greater conservation gains may be obtained, for example by oil palm managers, by setting aside forested buffer zone, of good quality forest, lining the edges of plantation boundaries and larger, continuous forest areas, particularly within protected areas. We believe such buffers will act as an extension of existing habitat for mammals and be more useful than maintaining small, random forest patches within oil palm landscape. Further work, however, is required in order to determine if this approach, which may lead to a greater length of edge habitat, will be suitable for species which have a strong tendency to avoid edge habitat.

Conclusions

Based on both mammal species richness and composition, the value of small isolated forest patches within oil palm plantations for terrestrial mammal species conservation is low. Mammals detected in the forest patches were mainly those species that are well-adapted to living in highly modified habitats and were generally of low conservation concern. Mammal species that are large-bodied and require large ranging areas, including low density species, were lost in the forest patches. Some mammal species may utilise forest patches inside oil palm plantations for foraging and to provide cover during resting periods, but for many mammal species, it is unlikely that oil palm habitats, including forest fragments within oil palm landscape, alone is able to support viable populations in the long-term. Many of the mammal species detected in the forest patches in this study were likely only transient in the oil palm habitat and their existence in this habitat were partly due to the contiguity of the study areas with an extensive natural forest area. Although our study may not necessarily represent other areas, findings of our study supported the idea that large continuous forest areas are essential requirements for the long-term survival of many terrestrial mammal species in tropical forests on Borneo, particularly species that are of high conservation concern. Such forest areas should be conserved wherever they still exist.

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