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Animal use of rehabilitated formerly fire damaged peat-swamp forest in western Sabah, Malaysia

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Abstract. Peat-swamp forests harbour diverse animal communities, but they are also highly prone to forest fires. Between January 2017–February 2018, we carried out a camera trapping survey of animals in a mixed peat-swamp forest partly affected by El Niño driven forest fires in 1998. This survey was conducted in the Klias Forest Reserve (KFR), of western Sabah, Malaysian Borneo. In addition to natural regeneration, the burnt areas in this peat forest have undergone active forest rehabilitation since 2006, including enrichment planting with indigenous tree species. We identified 22 animal species (16 mammals and six birds) in the surveyed areas including common and rarer species of high conservation value. The richness of animal species detected in the rehabilitated (formerly burnt forest) and the nearby intact (unburnt) forest areas was generally comparable. The similarity of detected animal species composition in each forest condition was also high (74% for all animal species combined; 86% for mammal species). Additionally, six of the seven most frequently photographed species did not show any significant difference in daytime and nighttime activity patterns in the rehabilitated as compared to intact forest. Interestingly, mousedeer species (*Tragulus napu* and *T. kanchil*) were found to be significantly more active during the daytime in intact (unburnt) forest compared to the rehabilitated. However, we suspect higher daytime mousedeer activity in intact areas is a behavioural adaptation to increased hunting pressure at night in this forest rather than a result of the local habitat conditions. Overall, our findings suggest that the rehabilitated mixed peat-swamp forest burnt 20 years ago, acts as an important functional extension to the intact forest of the KFR ecosystem and provides useful additional habitat for animal conservation.

Key words. peat-swamp forest, forest fire, camera trapping, habitat use, activity patterns, Klias peninsula

INTRODUCTION

Forest fires are well known to have immediate adverse impacts on many wildlife species due to the direct effect of the fire itself or indirectly through loss of food resources or other critical habitat resource needs (Lunney et al., 1987; Boer, 1989; Rochadi et al., 2000; Yeager et al., 2003; Barlow & Peres, 2004). But decades after fire damage, changes in vegetation structure and plant types may continue to affect various animal species differently, leading to differences in relative population size and/or distribution, thereby altering the overall faunal community composition (Rochadi et al., 2000; Yeager et al., 2003; Barlow & Peres, 2004). Although the effects of natural forest regeneration on animal communities in burnt forest have been documented to some extent, there is still a dearth of information on long-term faunal responses to forests that have undergone assisted rehabilitation following forest fires, particularly in peat-swamps (Yeager et al., 2003; Barlow & Peres, 2004).

Peat-swamp forests are found extensively throughout Southeast Asia (Posa et al., 2011). They are important as a reservoir for many unique animal and plant species (Cheyne & McDonald, 2011; Sasidhran et al., 2016), and provide essential ecosystem services on a broad scale, such as mitigating floods locally, influencing the climate far beyond their borders, and even acting as a global carbon store (Page et al., 2002; Sebastian, 2002; Koh et al., 2009; Posa et al., 2011). Yet, peat-swamp forests are being degraded and lost at a rapid rate due to human population expansion, agricultural and infrastructural development, and from fire (Yule, 2010; Posa et al., 2011; Miettinen et al., 2012; Adila et al., 2017).

The threat of forest fire to peat-swamp forests is particularly evident during extended droughts. For example, fires associated with the exceptional drought caused by an El Niño climate cycle in 1997–1998 devastated much of Southeast Asia (McPhaden, 1999; Murty et al., 2000). During that period, fire destroyed large areas of peat land in Kalimantan, Indonesia (in the south and eastern parts of Borneo) (Boehm et al., 2001). In the Malaysian state of Sabah (in northern

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Borneo), severe fires occurred in the peat-swamp forests at two reserves in the Klias Peninsula in April 1998 (UNDP/GEF, 2001); (1) Binsulok Forest Reserve (12,106 ha) was almost entirely devastated by the fire, while approximately 10% of the nearby (2) Klias Forest Reserve (KFR) (3,630 ha) was also destroyed (Phua et al., 2007).

In 2002, a federal initiative to recognise the conservation value of peat-swamps as fragile ecosystems that harbour highly significant biodiversity and important ecosystem services was launched in Malaysia (Nik et al., 2007). As one of the few remaining peat-swamp forests in the country, and given its importance to the overall hydrological function and ecological integrity of the Klias Peninsula locally and regionally, the KFR was identified as a critical site for development of an integrated peat-swamp forest management plan (Nik et al., 2007). Information provided by the KFR manager Mr. Nur Zaili Ali revealed that following the endorsement of this directive, rehabilitation of fire degraded habitats began in 2006 in and around KFR (Nur Zaili Ali, personal communication).

Although more than 12 years have passed since the initiation of this forest rehabilitation programme, no ecological survey to discern the effects and/or value of the rehabilitated forest for biodiversity conservation in KFR on animal communities has been completed. Given the increasing trend of disturbance and habitat loss in the Klias peninsula region (Kamlun et al., 2016), the expected effects of normal El Niño cycles, as well as the intensifying potential of global warming-mediated climatic changes (Struebig et al., 2015; Thirumalai et al., 2017), a comparative study into the presence, distribution, and activity patterns of animal species in pristine as well as degraded peat-swamp habitats is essential for effective land-use planning and conservation management strategies in this region. The findings of such research can serve to identify where suitable habitats are still present as well as where habitats, degraded by fires or other causes, could be rehabilitated. This will facilitate not only preservation of important native animal species of high conservation concern in peat-swamp forest, but also conservation of key animal community assemblages necessary to maintain overall habitat functionality in the long term (Tobler et al., 2008; Bernard et al., 2016).

In this study, we present the first camera trap survey results of animal species found in the mixed peat-swamp forest of KFR that has been altered by El Niño drought-driven forest fires two decades ago (in 1998) and has since been rehabilitated by enrichment planting (beginning in 2006). We describe general forest condition differences and compare the richness and composition of animal species in the rehabilitated and adjacent intact (unburnt) forests. We also investigate the intensity of habitat-use as well as temporal activity patterns of some animal species common to both forest conditions. Our aim was to ascertain the animal community response to the rehabilitated forest areas, and thereby assess the usefulness of the rehabilitated areas for animal conservation. We predicted that species richness and composition of animals, as well as their habitat-use intensity and temporal activity pattern in the rehabilitated formerly burnt forest, would be different from that of the intact forest due to their different forest structure and conditions (Barlow & Peres, 2004; Adila et al. 2017).

METHODS

Study sites. The KFR (5°9′32″N; 115°40′22″E) is located on the Klias Peninsula, in southwestern Sabah, Malaysian Borneo (Fig. 1). It occupies an area of 3,630 ha of flat land with elevations ranging mainly between 0–10 m above sea level (Bernard et al., 2019). The major vegetation type in KFR is mixed peat-swamp forest with the most common canopy tree being *Dryobalanops rappa*. Other tree species, namely *Dactylocladus stenostachys*, *Madhuca motleyana*, and *Shorea platycarpa* are also widespread throughout the Reserve. These four tree species account for 70% of the standing basal area of the forest (Fox, 1972). About 40% of the area of KFR was selectively logged, mainly for the commercially valuable ramin tree, *Gonystylus bancanus*, from the early 1960s until gazettement as a Class I forest reserve in 1984. Since that time logging has been totally prohibited (Sabah Forestry Enactment, 1968). The remaining 60% (2,178 ha) of the KFR that was not logged remains largely intact (Nik et al., 2007). Most of the peatlands outside of the Forest Reserve have been cleared and drained for agricultural uses, i.e., rubber, oil palm, pineapple and other crops, while other areas have been converted to human settlements or left idle in a degraded condition (Phua et al., 2007). The KFR is bordered to the north, northwest and northeast with contiguous mature oil palm plantations (>10 years old). During the catastrophic El Niño drought-induced forest fires of April 1998 most affected areas in KFR were burnt to the ground with only a few standing trees remaining (Mohamed et al., 2000; H. Bernard, personal observation). As far as can be determined, the affected areas were burnt only once. In addition to natural regeneration (from 1998 to 2006), an active program of forest rehabilitation and enrichment was initiated in 2006 until 2010 in the burnt areas as part of the UNDP/GEF Peat-swamp Forest Project in collaboration with the Forest Research Institute of Malaysia (FRIM) and Sabah Forestry Department (UNDP/GEF, 2001). Enrichment planting was conducted using mainly indigenous trees: *D. rappa*, *G. bancanus*, and *Lepisanther* spp. Trees were planted in blocks ranging in size between 4–25 ha with a density of c. 400 trees/ha and were subjected to continuous active forestry management (Nur Zaili Ali, personal communication). A total of 300 ha has been rehabilitated (Nur Zaili Ali, personal communication).

Identification of rehabilitated versus intact forests. We identified forest areas burnt in 1998 and defined the rehabilitated and intact forest areas in 2016 in KFR using the Normalised Difference Vegetation Index (NDVI) of the study area in 1998 and in 2016, respectively. We used Landsat5 and Landsat8 satellite images with ground pixel size of 30 m and no or minimal cloud cover, downloaded from Lansat-Look (https://landsatlook. usgs.gov/viewer.html), to represent the forest cover of the study area in 1998

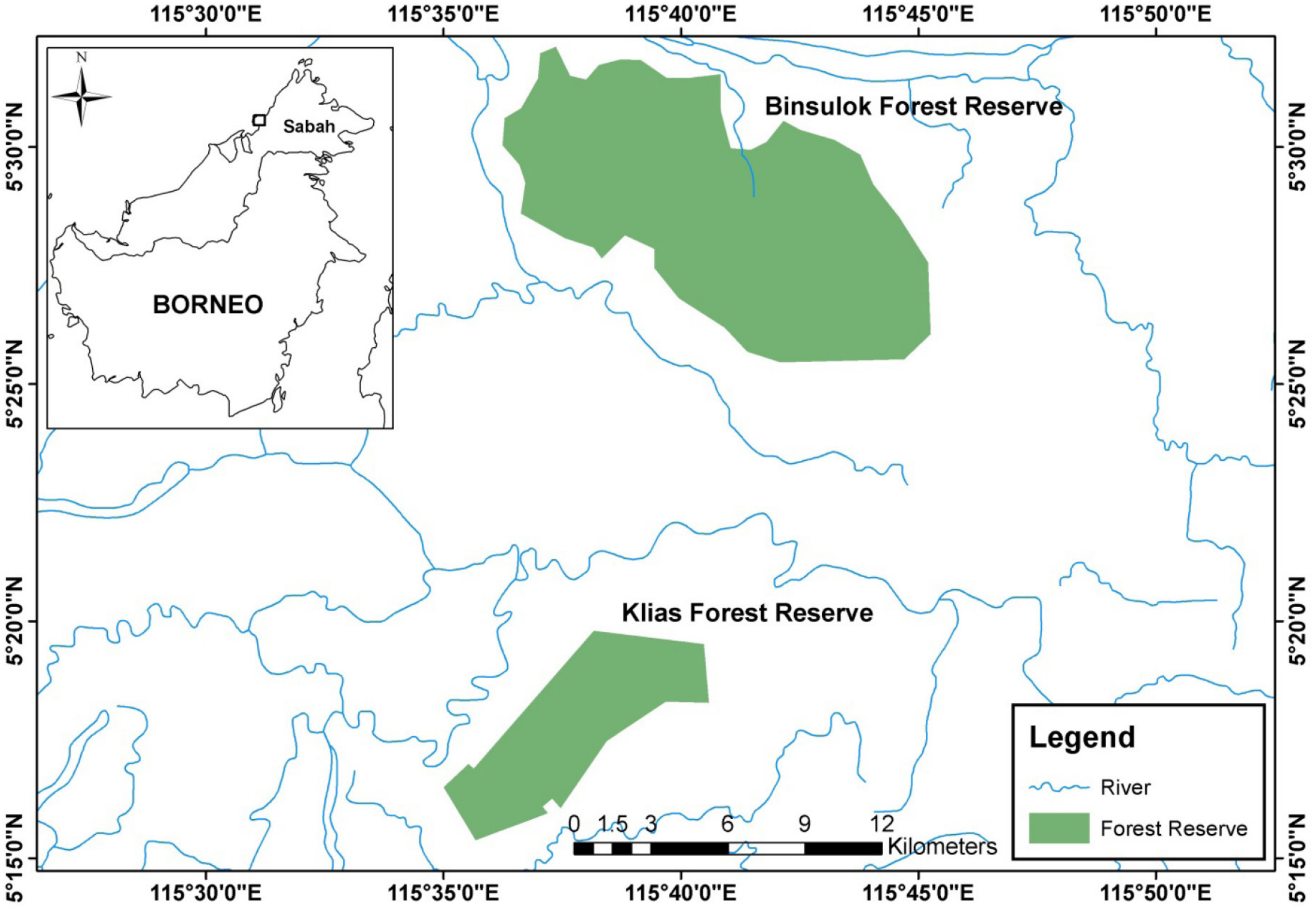

Fig. 1. Klias Forest Reserve and Binsulok Forest Reserve located in the Klias Peninsula in south-western Sabah, northern part of Malaysian Borneo (inset).

and 2016. We calculated the NDVI based on the ratio: (NIR-Red)/(NIR+Red), where, "NIR" = near-infrared band; and "Red" = red band. We standardised the NDVI values to range between −1 and +1 with values approaching +1 generally indicating higher vegetation cover. Before calculating the NDVI, we performed an atmospheric correction for all images. We calculated the NDVI using ENVI (ver. 5.5, ESRI) and conducted spatial analysis using ArcGIS 10.2.2 (ESRI). In addition, we verified the rehabilitated and intact forest areas based on direct observations of the forest structure in the field (2016) by measuring canopy height (using a laser range finder BOSCH DLE70 Professional) and estimating canopy cover (using a densiometer) at 20 points located at 20 m intervals along two 200-m long line transects placed in rehabilitated and intact forests, respectively.

Animal surveys. We used camera traps designed to detect mainly medium- to large-sized terrestrial animals in order to measure animal presence. We established 10 camera trap points in rehabilitated areas and 10 camera trap points in intact areas covering approximately 730 ha in the northern part of KFR (Fig. 2). We placed all cameras along newly cut trails in the forest and at random locations near animal trails. We used automatic motion-triggered, digital camera traps (Bushnell HD Trophy Cam model 119537 and Cuddeback Capture IR cameras). We placed only one camera at each camera trap point. All cameras were attached to trees, between 0.25–0.4 m (mean = 0.29 m) from the ground. Due to difficulties associated with access in dense and swampy habitats, distances between camera trap points were not uniform but ranged between 0.24–2.87 km (mean = 0.75 km). We marked the precise geographic locations of all cameras in the field using a handheld GPS unit (Garmin eTrex) and plotted them on satellite maps of the study area. We set Bushnell cameras at high sensitivity to take 3 photographs at every trigger with no time delay between triggers. Since the Cuddeback cameras can only take one shot per trigger and had no setting for sensitivity they were set accordingly. The overall survey period was 10 months between January 2017–February 2018. We left the cameras at each location for at least 2.5 months before moving them to a new location to maximise the sampling area that was covered in two survey sessions in the following sequence: rehabilitated areas (5 camera trap points from January–April 2017; 5 camera trap points from November 2017–February 2018) and intact areas (5 camera trap points from January–April 2017; 5 camera trap points from September–December 2017). We used the same number of Bushnell (4 units) and Cuddeback (1 unit) cameras at each habitat type per camera trapping session throughout all survey intervals. Over the survey duration rainfall was normal and there was no prolonged drought. All cameras recorded photographs over 24 hours per day. We did not use any bait or lures near cameras. We checked all cameras once a month to retrieve images and replace batteries when necessary.

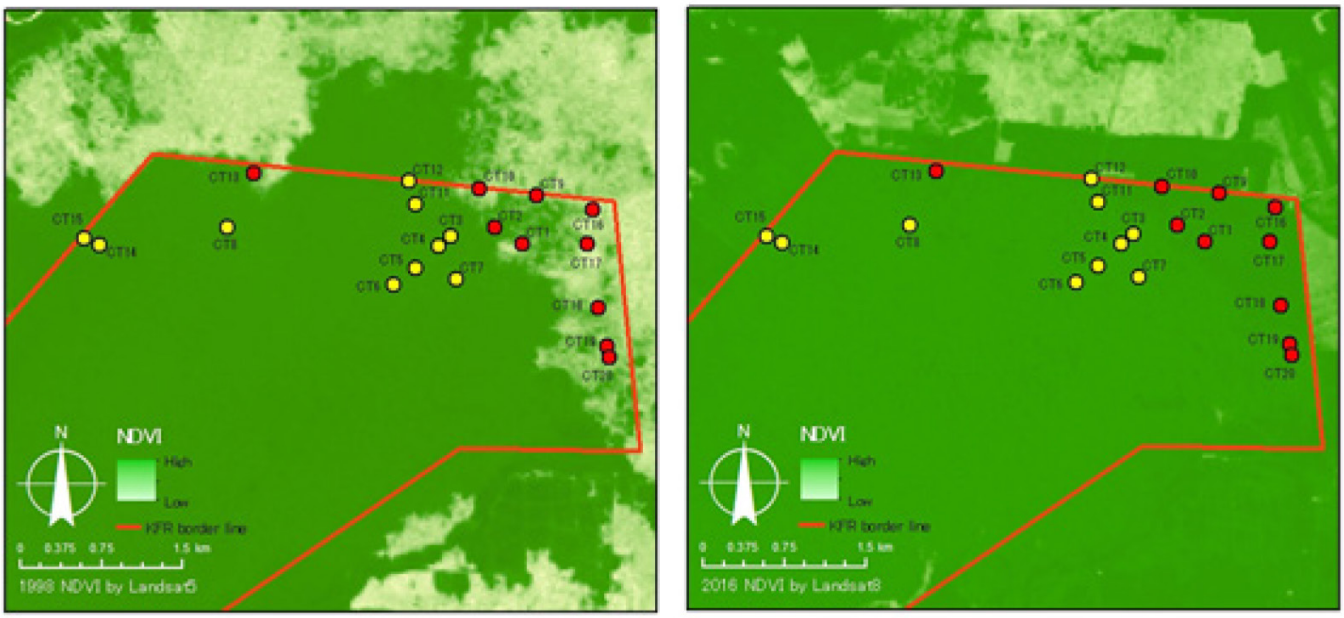

Fig. 2. Maps of the Normalised Difference Vegetation Index (NDVI) of the northern part of Klias Forest Reserve indicating the burnt forest areas (white) in 1998 (L) and the same study area in 2016 including oil palm plantations (white) in the north and eastern part of the reserve (R). Red circles indicate locations of camera trapping points in rehabilitated/burnt areas; Yellow circles indicate locations of camera trapping points in intact/unburnt areas.

Data analysis. We used Phillips & Phillips (2016) for mammal species identification and Phillips & Phillips (2011) for bird species identification. We determined the global or regional conservation status of each species based on the IUCN Red List of Globally Threatened Species (IUCN, 2018). State protection status accorded to the species, i.e., Totally Protected Animal or Protected Animal, was determined based on the Wildlife Conservation Enactment of the state of Sabah (WCE, 1997). Some birds and small mammals such as rats, squirrels, treeshrews, and bats, were too small for positive species identification. In these cases, we grouped them into general animal classes. We also treated the two mousedeer species, *Tragulus napu* (greater mousedeer) and *T. kanchil* (lesser mousedeer), as a single genus (*Tragulus* spp.) as they were often not readily distinguishable in the photographs. All photographs from camera traps were date- and time-stamped. We considered each photograph captured of an animal species at the same camera trap point more than 1 hour apart, as an independent capture event (Bernard et al., 2013; Mohd-Azlan et al., 2018). We disregarded group size, so a photograph of an animal species containing more than one animal was considered a single independent photographic event. We calculated the camera trapping effort by the number of trapping-days when each camera trap was functional.

We calculated the photographic capture rate per 100 camera trapping-days for each animal species (or class or genus) (D_i) to evaluate their habitat use intensity at different camera trap points. We used the following basic formula: $D_i = (N_i / \sum TD) \times 100$, where N_i is the total number of independent photographic events recorded of species i (or class i or genera i) and $\sum TD$ is the total number of functional camera trapping-days at a camera trap point or at all camera trap points combined representing each forest condition (i.e., rehabilitated or intact). We evaluated animal species richness using the observed species number.

To determine the sampling saturation in rehabilitated and intact areas, we used rarefied species accumulation curves of the number of observed species as a function of the cumulative number of independent photographic events representing the sampling effort. We constructed the observed species accumulation curve using EstimateS version 9.10 with upper and lower limits of the 95% Confidence Interval based on 100 random iterations (Colwell, 2013). We assumed that sampling saturation was met when the observed cumulative number of animal species reached an approximate asymptote with the cumulative number of independent photographic events. We calculated the percentage similarity of species assemblage composition detected between the rehabilitated and intact areas using the Sørenson similarity coefficient (Sørenson, 1948) calculated in EstimateS.

We also analysed the daily activity patterns of animal species that were frequently photo-captured and compared them between rehabilitated and intact areas for each species (or genus). We assumed that daytime and nighttime length was equal at our study sites: 12 hours from 0600–1800 hours (daytime) and 12 hours from 1800–0600 hours (nighttime). We assumed that the number of independent photographs captured at different times of the day of a given species (or genus) was correlated to their 24-hour daily activity patterns. We performed Pearson's Chi-squared tests with Yates' continuity correction to determine whether the activity patterns (frequencies of independent photographs captured during the daytime and nighttime) of a species (or genus) were influenced by the habitat where they occurred (i.e. rehabilitated or intact forest) (Zar, 2010). We conducted all inferential statistical analyses using the statistical software

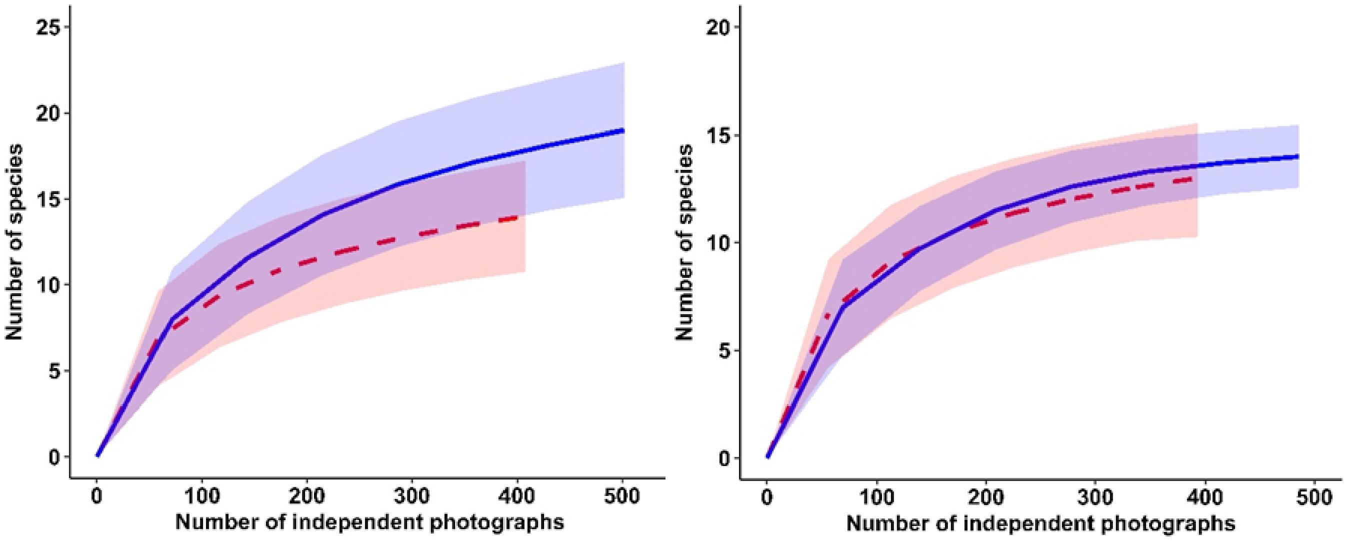

Fig. 3. The observed species accumulation curves in rehabilitated forest (solid lines) versus intact forest (dashed lines) and their 95% Confidence Intervals for all animals detected (L) and for mammal species only (R) in Klias Forest Reserve. The curves were constructed using an abundance-based rarefaction approach with 100 randomisation runs in EstimateS (Colwell, 2013).

R, version 3.1.3 (R Development Core Team, 2015). We considered a probability of *p*-value ≤ 0.05 as significant in all analyses.

RESULTS

There was a clear distinction between the burnt and intact forests identified using the NDVI based on images of the study area taken in 1998. This difference was not as discrete as that in images of the same area taken in 2016, indicating that the rehabilitated formerly burnt forest areas had recovered to some extent by 2016 (Fig. 2). However, based on direct observation on the ground in 2016, the differences in forest structure between conditions were much more apparent – the average canopy height (mean ± s.d.) of the rehabilitated areas was 12 ± 5.12 m, compared to intact areas (23 ± 4.22 m), and the canopy cover in the rehabilitated areas was 43 ± 12.15%, compared to intact areas (78 ± 4.22%).

Because of camera malfunction and loss due to theft, only 14 (7 in rehabilitated and 7 in unburnt areas) camera trap points, of the 20 initially set up, produced sufficient data for analysis. All functional cameras were Bushnell cameras. The total combined functional camera-trapping effort of 1,227 camera trapping-days (average individual camera trapping effort: 88 camera trapping-days; range: 78–100 camera trapping-days) yielded 795 independent digital photographs representing at least 22 fauna species (16 mammals and six birds) from the northern part of KFR. Long-tailed macaque (*Macaca fascicularis*), bearded pig (*Sus barbatus*), moon rat (*Echinosorex gymnurus*), mousedeer (*Tragulus* spp.) and pig-tailed macaque (*M. nemestrina*) were the five most frequently photographed species accounting for 76% of the total independent photographs captured (Table 1). Eighteen species were listed on the IUCN Red list; five species were listed as threatened by extinction (Vulnerable, Endangered, and Critically Endangered), 12 species not threatened (Least Concern, and Near Threatened) and one species has not been evaluated. In addition, two species are listed as Totally Protected Animals and 12 species as Protected Animals under the Sabah Wildlife Conservation Enactment (WCE, 1997). Two species are endemic to Borneo: proboscis monkey (*Nasalis larvatus*) and crested fireback (*Lophura ignita*) (Table 1).

Cameras in rehabilitated areas recorded a minimum of 20 animal species from 432 independent photographs over 578 functional camera trapping-days, and in intact areas, a minimum of 15 animal species from 363 independent photographs over 649 functional camera trapping-days. The observed species accumulation curves appeared to be reaching asymptotes for both areas indicating that the sampling saturation of the camera trapping in this survey was reasonably high (Fig. 3). In general, more species were recorded in the rehabilitated areas than in intact areas, although a higher number of animal species in the rehabilitated areas were detected as singletons (these were mainly bird species). When the rarefied species accumulation curves were constructed only for mammal species, the species richness was comparable for both rehabilitated (15 species) and intact forests (13 species). The percentage of similarity of all animal species (mammals and birds) detected in rehabilitated and intact areas calculated using Sørenson similarity coefficient was 74.3%, whereas the percentage similarity for mammal species only was 85.7%.

In terms of temporal activity patterns of animals, we found that for six of the seven animal species examined, their activity patterns were independent of the habitat type where they were detected (Table 2; Fig. 4). However, the mousedeer species, *Tragulus* spp., were significantly more active during the daytime in intact forest as compared to the rehabilitated habitat condition.

Table 1. Summary of animals photo-captured in rehabilitated and intact forest areas in the northern part of Klias Forest Reserve, Malaysian Borneo. NIP, number of independent photographs; SPR, photographic rates of species captured. IUCN, red list of globally/regionally threatened species, CR=Critically Endangered; EN=Endangered; VU=Vulnerable; LC=Least Concern; Na =assessment is not available for this species. WCE, Sabah Wildlife Conservation Enactment (1997) protection status, TP=Totally Protected; P=Protected; G=Game Animals. (E)= denotes Bornean endemic species.

Class	Order	Family	Scientific Name	English Name	NIP Rehabilitated Forest	NIP Intact Forest	Total NIP	Overall SPR	IUCN	WCE
MAMMALIA	Carnivora	Mephitidae	*Mydaus javanensis*	Sunda stink badger	5	1	6	0.49	LC	P
		Viverridae	*Hemigalus derbyanus*	Banded palm civet	0	4	4	0.33	NT	P
			Paradoxurus hermaphroditus	Asian palm civet	18	12	30	2.44	LC	P
		Felidae	*Prionailurus bengalensis*	Leopard cat	7	0	7	0.57	LC	P
	Primates	Cercopithecidae	*Macaca fascicularis*	Long-tailed macaque	105	66	171	13.94	LC	P
			M. nemestrina	Pig-tailed macaque	33	37	70	5.70	VU	P
			Nasalis larvatus	Proboscis monkey (E)	3	10	13	1.06	EN	TP
	Cetartiodactyla	Cervidae	*Cervus unicolor*	Sambar deer	6	8	14	1.14	VU	G
		Suidae	*Sus barbatus*	Bornean bearded pig	56	82	138	11.25	VU	G
		Tragulidae	*Tragulus* spp.	Mousedeer	68	31	99	8.07	LC	G
	Eulipotyphla	Erinaceidae	*Echinosorex gymnurus*	Greater moonrat	65	63	128	10.43	Na	–
	Pholidota	Manidae	*Manis javanica*	Sunda pangolin	1	0	1	0.08	CR	TP
	Rodentia	Muridae	Rat	Rat	4	2	6	0.49	–	–
		Sciuridae	Squirrel	Squirrel	38	30	68	5.54	–	P
	Scandentia		Treeshrew	Treeshrew	6	6	12	0.98	–	–
	Chiroptera		Bat	Bat	4	0	4	0.33	–	P
AVES	Galliformes	Phasianidae	*Lophura ignita*	Crested fireback (E)	8	10	18	1.47	NT	P
	Columbiformes	Columbidae	*Chalcophaps indica*	Common emerald dove	2	0	2	0.16	LC	P
	Accipitriformes	Accipitridae	*Spilornis cheela*	Crested serpent eagle	1	0	1	0.08	LC	P
	Passeriformes	Pellorneidae	*Pellorneum capistratum*	Black-capped babbler	1	0	1	0.08	LC	G
		Pittidae	*Pitta moluccensis*	Blue-winged pitta	1	0	1	0.08	LC	P
		Rhipiduridae	*Rhipidura albicollis*	White-throated fantail	0	1	1	0.08	LC	G
		Total	22 spp.		432	363	795	64.79		

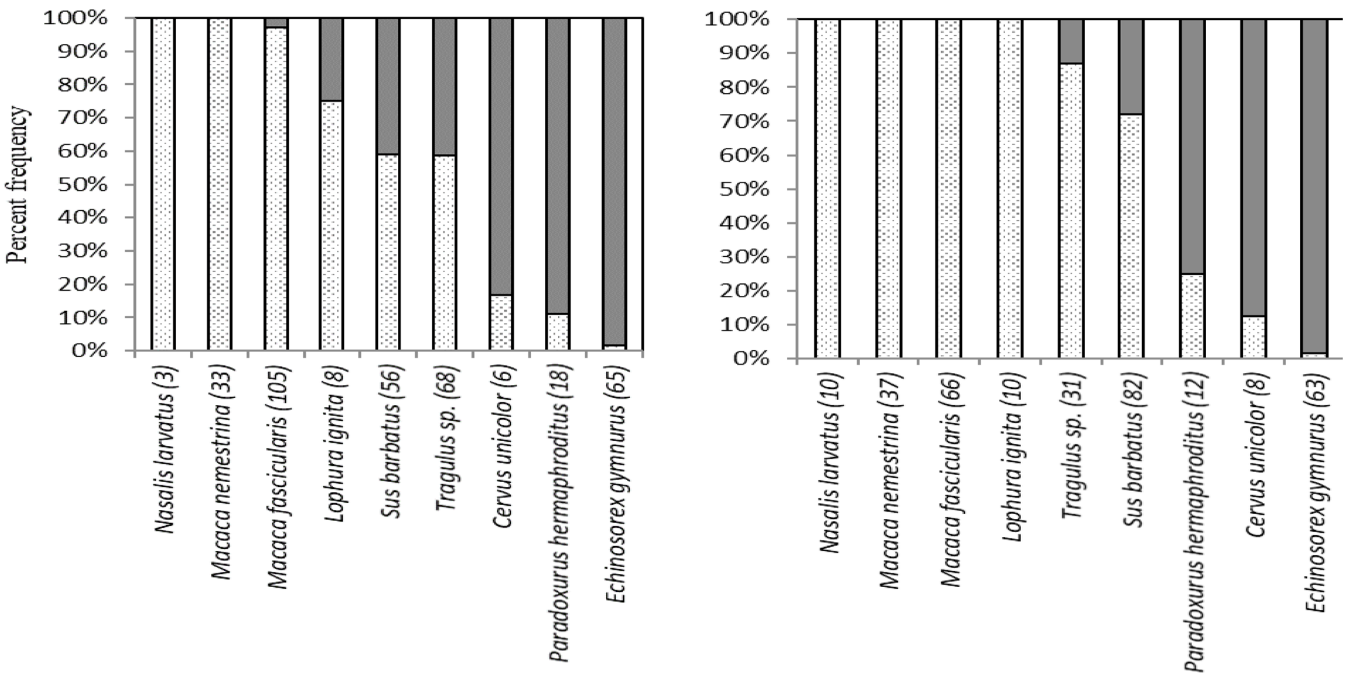

Fig. 4. Temporal activity patters for the nine most frequently photographed animal species in the northern part of Klias Forest Reserve, Sabah, Malaysia. Rehabilitated forest (L); Intact forest (R). Black bars indicate nocturnal activity; dotted bars indicate diurnal activity. Number in parenthesis represents number of independent camera trap records.

Table 2. Results of chi-squared 2 by 2 contingency table test to determine if a relationship between activity patterns of animal species (frequencies of independent photographs captured during the daytime and nighttime) and habitat type (i.e., rehabilitated or intact forest) was evident.

Species	**Chi-squared Value**	**d.f.**	***p*-value**
M. fascicularis	1.9194	1	0.1659
S. barbatus	2.5394	1	0.1111
E. gymnurus	0.0000	1	0.9822
Tragulus spp.	7.7809	1	0.0053**
M. nemestrina	NaN	1	–
P. hermaphroditus	1.0000	1	0.3173
L. ignita	2.8125	1	0.0935
R. unicolor	0.0486	1	0.8255
N. larvatus	NaN	1	–

Note: NaN indicates that analysis could not be performed because all animals were detected only during the daytime in both rehabilitated (burnt) and intact (unburnt) forests. ** indicates the relationship between activity patterns and habitat condition was significant: *p*-value <0.01.

DISCUSSION

Our results revealed a rich and diverse animal community inhabiting the mixed peat-swamp forest in the northern part of KFR, including areas that have been rehabilitated. We recorded common animal species, as well as many threatened and near threatened species of conservation importance regionally and globally. Many of the species are also listed in the local protected species list of the Sabah Wildlife Conservation Enactment (WCE, 1997). Our results also indicate that the richness and species assemblage composition of animals recorded in the rehabilitated and intact forests were generally comparable, suggesting that animal communities detected in the rehabilitated and intact forests in KFR were generally homogeneous.

Despite the fact that these rehabilitated forests remain structurally distinct from the intact (unburnt) areas in our study sites – rehabilitated forest generally had lower tree height, more open and highly irregular canopy than that of the intact forest, we observed remarkable similarity in animal species composition (74.3%) between habitat conditions, particularly with respect to mammalian fauna (85.7%). However, most of the animals (including birds, e.g., crested fireback), detected were predominately terrestrial species that do not depend on the forest canopy for movement or resources. This was not unexpected as all camera traps were positioned exclusively near ground level. Consequently, while we may have achieved sampling saturation in terms of representing the terrestrial animal community at our study sites, we have likely under-sampled others, especially true canopy specialists.

Given that fire-mediated change in vegetation structure due to forest fires even 20 years ago may have negatively impacted true forest canopy specialists in the rehabilitated forest disproportionately, and canopy-dependent species such as squirrels, primates and many bird species may actually represent a larger proportion of the total animal community living in peat-swamp forests (Phillips & Phillips, 2011; 2016), we propose further parallel comparison studies of canopy dependent species to be conducted. We also suggest further studies using a mixed method approach such as mist netting for birds and bats, and direct observations via day and night transect walks for diurnal and nocturnal canopy mammals including primates, to gather data that captures a wider range of animal habitat use (Azhar et al., 2011; Struebig et al., 2013; Bernard et al., 2014; Bernard et al., 2016).

Nevertheless, with respect to the data on more terrestrial animals captured in this study, the most frequently detected species showed no discernible differences between the rehabilitated and intact forest in terms of overall numbers and habitat use intensity. This suggests that resources used by animals detected in our camera trap surveys are found in comparable numbers in both forest conditions. Additionally, more open canopy found in the rehabilitated forest may also provide more favourable foraging opportunities for some of these species. For example, short vegetation including grasses that flourish on the forest floor in crown-gap areas and near forest edge likely provide important food sources for the mousedeer and sambar deer (Matsubayashi et al., 2003; Brodie et al., 2015). Many plants in crown-gap areas also produce fruits (Whitmore, 1998) and these are useful resources for animals including the mousedeer, bearded pig, pig-tailed and long-tailed macaques (Matsubayashi et al., 2003; Jati et al., 2018; Granados et al., 2019).

Long-tailed macaques are the most common monkey in disturbed and secondary forests, and thrive at forest edges and in other disturbed or modified environments (Sha & Hanya, 2013). In our study, they were observed frequently at the border between the rehabilitated and intact forest. Although predominantly frugivorous, long-tailed macaques are highly adaptable and readily shift their diets with availability. For example, in severe drought they have been observed to exploit insects that become more abundant in post-burnt areas of lowland dipterocarp rain forest in Kutai National Park, Kalimantan, Indonesia (eastern Borneo) (Berenstain, 1986). Elsewhere, the total biomass of dung beetles was found to be higher in post-burnt areas in mixed semi-deciduous and lowland terra firma forests burnt 25 years ago in the northern Brazilian Amazon (Andrade et al., 2014). Casual observation suggests insects might also be more abundant in the rehabilitated peat-swamp forest in KFR as compared to the intact forest. Further studies are warranted to confirm whether an increase in insect abundance may also likely explain the frequent observations of the insectivorous moon rat, as well as omnivorous carnivores such as the Sunda stink badger, in the rehabilitated areas of our study (Samejima et al., 2016).

Continuous forest connects the rehabilitated and intact areas, and there were no gaps devoid of vegetation between the rehabilitated and oil palm habitats to the north east of the KFR, hence permitting unrestricted movement of animals between these areas. Therefore, some of the animals recorded in the rehabilitated areas in KFR may be transient in this habitat, i.e., using this area as a corridor to commute between the oil palm plantation and the intact forest in the interior of the reserve. Bearded pigs, for example regularly utilise oil palm plantation habitats for foraging as oil palm fruits are a reliable resource available all year-round (Yue et al., 2015; Love et al., 2018). We observed several active communal mud wallows used by bearded pigs in an open area and under tree shade in rehabilitated areas, suggesting that they were also using the rehabilitated forest for resting, perhaps during the daytime to avoid higher temperatures in more degraded habitat with less canopy cover. The leopard cat is another example. Leopard cats have been observed to preferentially use oil palm plantations, possibly to hunt murid prey as they are recorded in greater numbers in oil palm plantations compared to surrounding natural forests (Rajaratnam et al., 2007; Chua et al., 2016). Even so, leopard cats may still use natural forest habitats as refuge and breeding sites (Rajaratnam et al., 2007; Yue et al., 2015). The common palm civet also exhibits a similar habitat use pattern to leopard cats, i.e., utilising the oil palm as a foraging site, and the adjacent forest as resting sites (Nakashima et al., 2013).

In terms of activity patterns, our study revealed that temporal activity patterns of all but one animal genus (mousedeer) detected were unaffected by forest condition. Though well known to be active both during the daytime and nighttime (Kitamura et al., 2010; Gray, 2018), activity patterns of mousedeer (both *T. napu* and *T. kanchil*) in Borneo determined by camera trapping methods appeared to be predominantly nocturnal (Mohd-Azlan & Lading, 2006; Bernard et al., 2013; Ross et al., 2013; Mohd-Azlan et al., 2018). However, in our study, mousedeer in KFR were predominantly diurnal. Interestingly, mousedeer in the rehabilitated forest were less diurnal than in the intact forest. This suggests that mousedeer forage or travel to some extent at night in the rehabilitated areas. The unexpected finding of an apparent altered pattern of daytime activity in the more stable habitat condition in our study may actually be an adaptive behavioural response to avoid nighttime hunting by humans, rather than a function of habitat condition. Some large game mammals (e.g., wild pigs and deer) have been found to shift their activity periods to avoid human disturbance, such as hunting (Griffiths & van Schaik, 1993; Little et al., 2016). We encountered several incidences of human encroachment inside the border of KFR, most likely by illegal hunters, but only in intact forest sites in the northwest and western borders of KFR. The rehabilitated forest sites are mainly located in the eastern border of KFR, near the Sabah Forestry Department's field station. Therefore, hunters may be less likely to enter the rehabilitated forest from the east side to hunt animals in the forest reserve at night, explaining the greater tendency of nocturnal activity patterns of mousedeer in this forest. This result highlights the need to consider other precipitating factors in addition to habitat condition as potential triggers of observed behavioural changes. Interestingly, based on radio-tracking and camera trapping methods in two protected forest sites in eastern Sabah, mousedeer were also found to be mainly active during the day and resting at night (Matsubayashi et al., 2003; Matsubayashi & Sukor, 2005). Given our results, it is perhaps useful to consider that hunting may be more practiced in some protected forests than is often assumed.

In conclusion, this study on habitat use 20 years after loss of forest to fire and about 10 years after enrichment planting, indicates that the rehabilitated peat-swamp forest areas in KFR are serving as a functional extension to the adjacent intact forest, providing useful habitat as foraging and refuge sites, and as movement corridors for many threatened and near threatened species of regional and global conservation importance. The fact that the overall mainly terrestrial faunal community composition detected by camera traps in our study has such great overlap (> 70%) between intact adjacent unburnt forest also provides a good baseline for monitoring and conservation management of other animal assemblages in these local rehabilitated areas in the future. Finally, we also detected illegal human activities taking place in the KFR within the intact forest areas, hence raising management concerns and highlighting the need for more law enforcement activities in the area especially and perhaps counterintuitively in the more intact forest. The fact that mousedeer activity patterns were more consistent with expected normal behavioural patterns in areas closest to the forest patrol base also emphasises the importance and effectiveness of local patrol presence in the area.

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