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Review paper

Mammalian communities as indicators of disturbance across Indonesian Borneo

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ABSTRACT

Using camera traps at eight grids across Indonesian Borneo we show how mammalian species assemblages can provide reliable information about how disturbance affects a forest. This enables us to use the large mammal community structure at each site to assess the impacts of human disturbance and habitat variables. Occupancy ranged from 0.01–0.77 with pig-tailed macaques, muntjac, orang-utans, sun bears, bearded pigs and common porcupines consistently having an occupancy of >0.5. These large mammals were generally making use of the whole forest surveyed and avoided the forest edge in only a few grids. A General Linear Model with general contrasts and survey effort as a covariate was performed to assess the impact of different variables. Logging and hunting were positively associated with low species number ($F = 6.3$, $p = 0.012$ and $F = 5.4$, $p = 0.003$ respectively). Logging and hunting contributed to a low % of carnivorous species ($F = 1.5$, $p = 0.021$ and $F = 4.8$, $p = 0.041$ respectively) and a higher % of IUCN Endangered and Vulnerable species ($F = 5.9$, $p = 0.044$ and $F = 5.0$, $p = 0.044$ respectively). The presence of burnt areas within the study grids was positively associated with reduced species numbers ($F = 5.3$, $p = 0.018$) and reducted % of carnivorous species ($F = 6.8$, $p = 0.023$) but not the % of IUCN Endangered and Vulnerable species. This is likely a result of burnt areas reducing the area of suitable habitat for many mammals. The proximity of the grids to roads, villages, rivers and presence of logging camps have been proposed as suitable parameters to indicate disturbance. In our study none of these parameters significantly affected the total species numbers, % of carnivores, and % of IUCN concern (Endangered and Vulnerable), nor did the protected status of the forest. We have identified 4 species as specific indicators whose presence or absence can help determine the type and/or extent of forest disturbance and/or be a proxy indicator for the presence of other species. Leopard cat (*Prionailurus bengalensis*) and pig-tailed macaques (*Macaca nemestrina*, generalists); sambar deer (*Rusa unicolour*, large, wide-ranging herbivores) and clouded leopards (*Neofelis diardi*) as a proxy for at least 2 of the smaller felid species.

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Contents

1. Introduction

Logging continues at a rapid rate in many tropical forests and has mixed effects on forest animal diversity (van Niewstadt et al., 2001; Wells et al., 2004; Meijaard et al., 2005; Wilcove et al., 2013). The effects of logging also change over time. Species composition in logged forests approaches that of unlogged forests just a few decades after logging has ceased (Danielsen and Heegaard, 1994; Slik and Verburg, 2002; Brodie et al., 2014). Selectively logged forests are becoming an increasingly dominant component of many tropical landscapes and yet, the conservation value of selectively logged tropical forests is less understood (Burivalova et al., 2014) than those of more dramatic land cover changes, such as deforestation driven by agriculture or tree-plantation developments (Estrada and CoatesEstrada, 1996; Meittinen et al., 2012).

Hunting occurs over even larger areas in the tropics than logging, and often, though not always, accompanies logging (Waltert et al., 2002; Brodie et al., 2014). It is also important to determine whether impacts of logging and hunting are correlated across species. Certain taxa, particularly large herbivores, may be vulnerable to extirpation due to both logging and hunting (leading to a positive correlation between the impacts of logging and hunting) or susceptible to either hunting or logging but not the other (no correlation) (Ripple et al., 2015).

Sundaland, encompassing the Malay Peninsula, as well as the islands of Borneo, Java, and Sumatra, contains one of the richest concentrations of biodiversity on earth, and preserving it is a priority for global biodiversity conservation (Myers et al., 2000). The island of Borneo covers less than 0.2% of the earth's land surface (743,330 km^2), yet is home to 4% of the world's plant species and 5% of birds and mammals (MacKinnon et al., 1996b) including up to 15,000 species of flowering plants (as many as the whole African continent), 3000 species of trees, 222 species of mammals and 420 species of resident birds (MacKinnon et al., 1996b). It is also home to 13 non-human primate species, eight of which are endemic (Groves, 2001; Brandon-Jones et al., 2004).

Borneo's biodiversity is under threat from increasing anthropogenic disturbances such as mining and logging, land conversion for monocultures such as oil palm plantations and forest fires (Aldhous, 2004; Fuller et al., 2004). In addition, indirect destruction is caused by the infrastructure created to access mines/plantations etc. such as roads and settlements and pollution from agricultural and extractive industry as well as artisanal mining. The impact of hunting animals for meat and/or as a response to human-wildlife conflict is poorly documented and understood (e.g. Voss et al., 2001; Matthews, 2006; Peres and Palacios, 2007; Ancrenaz et al., 2013; Ancrenaz et al., 2015; Brodie et al., 2014; Gaveau et al., 2014). Hunting of wildlife is perceived to be widespread across Kalimantan (e.g. Meijaard, 2001; Struebig et al., 2007; Harrison et al., 2011; Cheyne et al., 2013. We used questionnaires to complement the camera trap surveys and provide insight into attitudes to conservation and wildlife and potential impact of hunting (direct or indirect) on Sunda clouded leopards (*Neofelis diardi*) and other species. We sought to gain a better understanding of villagers' dependency on natural resources, impact on biodiversity and the identification of environmental changes as perceived by locals who might indicate possible threats to nature and communities. We present a single approach method using camera traps at grids with very varied management, protected status, habitat, accessibility and levels of human disturbance. We recognise that no single method is likely to be ideal for all purposes, or even suitable for use in all forests Harrison et al., 2012a). Instead, we chose the best and most consistent method, camera trapping, to (1) make use of all the data, (2) remove the reliance on one or two elusive species (Dufrêne and Legendre, 1997; Carignan and Villard, 2001) and (3) provide reference/baseline data.

Borneo is currently losing more than 500,000 ha of forest each year; one of the highest rates of forest loss in the world (Gaveau et al., 2009, 2014). The habitats most threatened by forest loss are the more accessible lowland areas, where species richness is greatest (MacKinnon et al., 1996a). This threatens even the best known of Borneo's wildlife; for example, of the Bornean orang-utan population at the beginning of the twentieth century, no more than 7% survive today (Rijksen et al., 1999). The continuing rapid expansion of oil-palm plantations is a particularly severe threat to all wildlife (Marshall et al., 2006; Fitzherbert et al., 2008; Wich et al., 2008).

Our objectives are (1) to assess the impact of forest type on the spatial distribution of mammals within and between grids, (2) to assess the impact of habitat on felid presence, species numbers and presence of threatened species, (3) to assess the impact of human disturbance on felid presence, species numbers and presence of threatened species and (4) to test the opportunity of using mammal communities to diagnose disturbance at a site and landscape level. The primary focus of the camera trapping was to obtain density estimates of clouded leopards; thus the cameras were placed in order to maximise clouded leopard detection. As a result, it is important to discuss in detail the felid data.

2. Study grids

In Murung Raya and Mungku Baru, the grids were considerably smaller due to access and time limitations (Table 1). The study sites differ in habitat type, altitude, size and human pressures which also impacted the size of the camera grid.

Sampling grids were selected to span gradients in habitat type, logging pressure, protected status, and human pressure, while maintaining spacing between cameras of at least 1 km. No systematic camera trap work had been carried out at any of the grids prior to this study. The eight grids representing a range of habitat types, protected area status, accessibility to humans, length of selective logging influence and perceived impact of hunting (Table 2). For ease of analysis the habitats were combined into four categories: Peat-swamp Forest (PSF), Lowland Dipterocarp/PSF, Lowland Dipterocarp and Lowland Montane.

All study grids were in Central or East Kalimantan (Fig. 1).

Unlogged areas were sampled in all study grids. Four grids had forest which was logged >20 years ago. Due to the size of area surveyed, all grids crossed several habitat types and all were affected by some level of disturbance. Burnt refers to areas where vegetation has been cleared by fire in the last ≤15 years and is recovering (Fig. 2).

3. Methods

3.1. Camera trapping

Cuddeback Capture IR® (Cuddeback Digital, Non-Typical) camera traps were placed along established trails and, where possible, watering areas, located so as to maximise the success rate of photographic 'detections' (Wilting et al., 2006; Gordon and Stewart, 2007; Cheyne et al., 2013). Two cameras were placed opposite each other, 7–10 m apart to create a paired station at each location with the aim of photographing each flank of the animal simultaneously. In Murung Raya and Mungku Baru only one camera was placed at each location. The passive infrared sensors were set at about 50 cm height. The Captures use an infrared flash. There are some logging roads in some of the study areas, all cameras were placed along established trails at cross-roads and near fallen logs or man-made boardwalks, which may facilitate felid movements during the flooded wet season (further information in Cheyne et al., 2013). As the focus of the overall study was on detection of clouded leopards and the smaller felids, and the cameras were only placed on the ground, we only include mammal species in this analysis as the detection of birds was too infrequent to provide a suitable sample size.

The grids were surveyed consecutively except for Sabangau which was surveyed concurrently with the Kutai and Lesan grids (Table 3).

Cameras were ideally set in a grid system with ±1 km between camera stations (Fig. 3). This layout was not possible in Bawan due to the disturbed nature of the forest and issues of water accessibility when setting the cameras thus the cameras were placed along established trails (Fig. 4). Non-random deployment of camera traps may interact with non-random space-use by animals, causing biases in our inferences about relative abundance from detection frequencies alone (Wearn et al., 2013). This limitation was alleviated in the present study by surveying a large number of locations (>60), surveying all available habitats types and sub-types and having the camera traps active for a suitable period of time (90–160 days).

3.2. Anthropogenic disturbance

We interviewed people living around the forest areas using questionnaires to determine if attitudes to hunting were reflected in evidence from the camera trap data. Questionnaire-based surveys were carried out to investigate the extent of direct removal of wildlife. All interviews/discussions took place at the same time the camera traps were in the area thus reflecting attitudes at the time of data collection (Table 4).

The research samples were derived using non-probability quota sampling (Kerlinger, 1986). The method was chosen to obtain an equally distributed sample over five different categories which were divided by age class (20–39 years, >40 years) and gender, and one category was for local 'governmental employees' such as the village head. Age classes were established

Table 1
Summary of habitat and climactic characteristics of each study area. Min and Max a.s.l. refer to placement of cameras not the overall altitude of the study area.

Grid	Habitat	Central latitude	Central longitude	Total Size of forest block/ landscape (km^2)	Average rainfall (mm/year)	Temperature range °C	Min a.s.l	Mean a.s.l	Max a.s.l	References
Bawan	Lowland Dipterocarp/Ombrogenous Peat-swamp Forest (PSF) mosaic	9 821 636	499 986	546	2500	12–35	35	72	93	Harrison et al. (2012b) and Wanelik et al. (2013)
Belantikan	Lowland Montane/Lowland Dipterocarp (LM/LD)	9 834 006	536 542	5000	2500	12–35	19	72	109	Sapari et al. (2005)
Kutai	Lowland Dipterocarp (LD)	5 457 920	570 690	2000	2500	12–35	41	152	246	Rodman (1977)
Lesan	Lowland Montane	1 774 120	527 897	110	2500	12–35	64	212	344	The Nature Conservancy (2011)
Mungku Baru	Lowland Dipterocarp	9 724 212	814 268	160	2500	12–35	30	60	80	Harrison et al. (2010)
Murung Raya	Lowland Montane. Pristine and remote	237 886	27 717	500	4000	24–35	80	150	231	McConkey and Chivers (2004) and Cheyne et al. (2012)
Sabangau	Ombrogenous PSF	9 739 536	820 452	5700	3000	12–35	12	29	30	Morrogh-Bernard et al. (2003) and Cheyne (2010)
Sungai Wain	Lowland Dipterocarp/Alluvial PSF	9 877 564	480 908	100	3000	12–35	35	69	86	Rustam and Tsuyuki (2012), Stark et al. (2012), Bersacola et al. (2014) and Gilhooly et al. (2015)

Table 2
Details of sampling of mammals for each study area in Kalimantan.

GRID	IUCN Protected status	Indonesian protected status	Total number of stations	Total area covered by cameras (km^2)	% of days > 1 hunter detected at each grid
Bawan	Not available	Not protected	63	67	10
Belantikan	VI	Nature reserve/Production forest	50	140	9
Kutai	II	National Park	52	124	3
Lesan	Not available	Nature reserve	70	110	15
Mungku Baru	Not available	Not protected	10	10	0
Murung Raya	Not available	Not protected	10	2	0
Sabangau	Not available	National Park/Conservation area	50	50	2
Sungai Wain	V	Nature reserve	79	100	1

Table 3
Survey dates for each grid (in date order).

Grid	Date start	Date end	Total days	Total number of cameras stations	Trap nights (number of active survey nights)
Bawan	09/09/2012	26/11/2012	78	63[b]	4146
Belantikan	23/02/2014	17/06/2014	114	50[b]	4583
Kutai	12/12/2012	23/03/2013	101	48[b]	3269
Lesan	15/07/2013	26/01/2014	195	70[b]	5548
Mungku Baru	02/02/2010	19/03/2010	45	10	200
Murung Raya	15/07/2011	20/09/2011	40	10	558
Sabangau[a]	01/03/2013	02/09/2013	185	30[b]	5487
Sungai Wain	17/05/2012	08/08/2012	83	79[b]	4729

[a] Cameras have been in place in Sabangau since May 2008 but for the purposes of comparison only data from a 6-month period were used.
[b] Indicates cameras were in pairs.

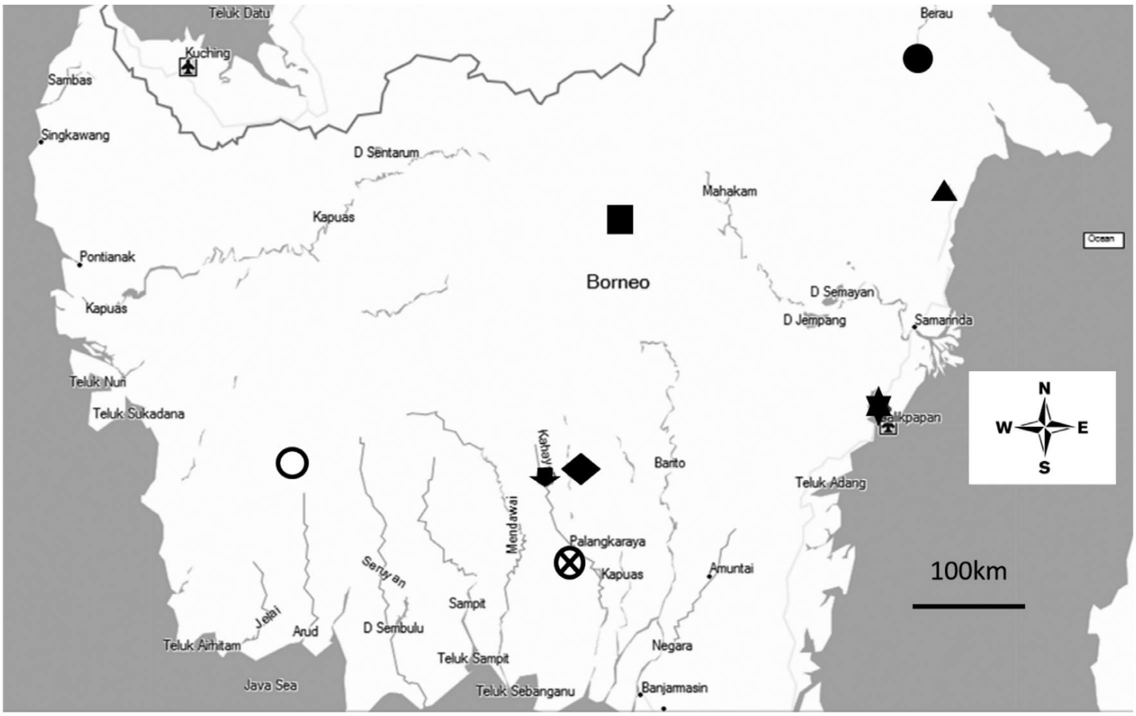

Fig. 1. Locations of the study grids. From west to east: White circle—Belantikan; Arrow—Mungku Baru; Cross circle—Sabangau; Diamond—Bawan; Square—Murung Raya; Star—Sungai Wain Circle; Triangle—Kutai National Park; Lesan—Black circle.

after consulting with several community members how the age-line (i.e. at what point people are considered 'young adult', 'middle-aged' or 'elderly') was defined within the villages, and the 'young adult (20–30 years)' and 'middle-aged (30–45 years)' classes were combined due to a small sample size. Questionnaires represented individual opinions and were adapted to local conditions by using information gained from informal and semi-structured interviews. Before starting

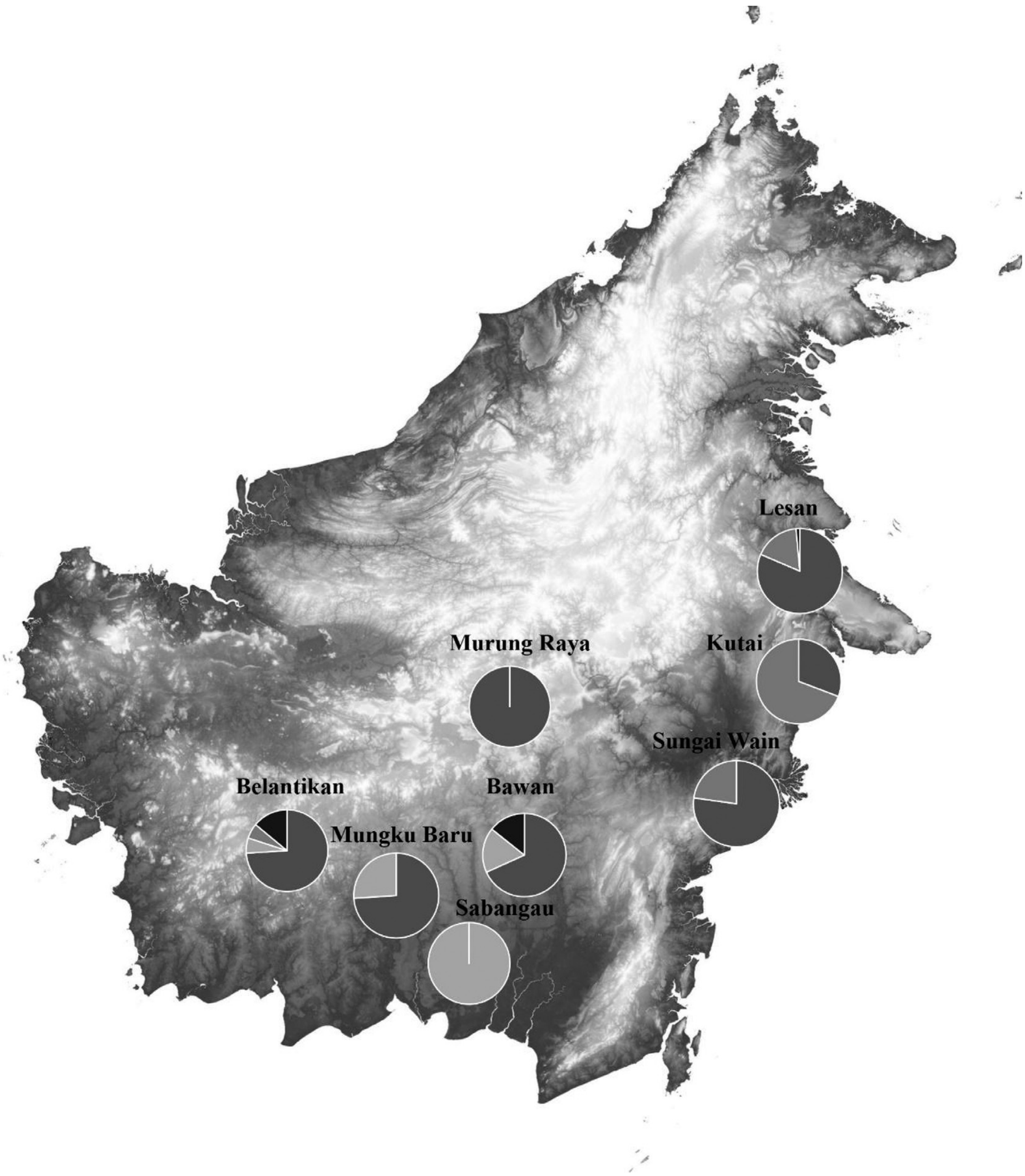

Fig. 2. Map of the study region in Indonesian Borneo showing for each study grid the proportion of camera stations in logged (light grey), burnt (mid-grey), undisturbed (dark grey) and plantation (black) forest. The elevation model is from Google Earth. White shading indicates high elevation; dark grey shading indicates low elevation. See Supplementary Information for a map detailing exact study grid location.

the sampling process in the villages, successive refinements of the questionnaire were tested three times on students to identify any questions which could bias the responses. To avoid bias, respondents were selected to come from different households, i.e. although some members of the same extended family were interviewed, they represented independent economic households. Furthermore, different households were selected to cover a wide range of different social levels. The questionnaires contained open as well as closed questions. For some issues, the contingent ranking method (Chambers, 1994) was applied (e.g. to determine the relative importance of different forest resources for peoples' livelihoods). Thus, each respondent was asked, for example, to choose the five most important aspects for their personal life. Afterwards the aspects were written on small cards and the respondent was asked to arrange them in ascending order of importance. Respondents were asked about all hunting activities to determine their impact on the natural community of which clouded leopards and their prey were part. Respondents were asked to rate their perception of availability of animals hunted by humans over a period of 10 years to account for possible depletion of prey in any given area. All data were collected by Indonesian researchers without foreign presence. Previous studies on which the questionnaire was based (Struebig et al., 2007; Harrison

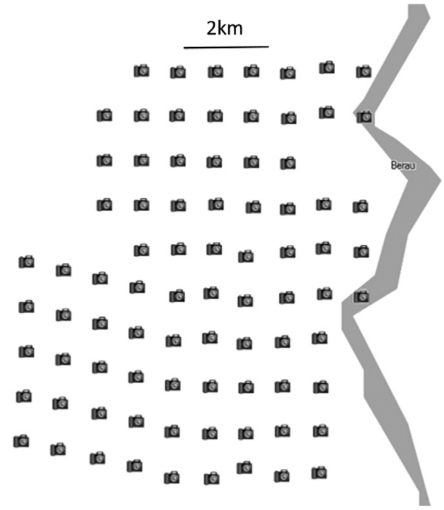

Fig. 3. Example of the standard camera trap grid system along in Lesan.

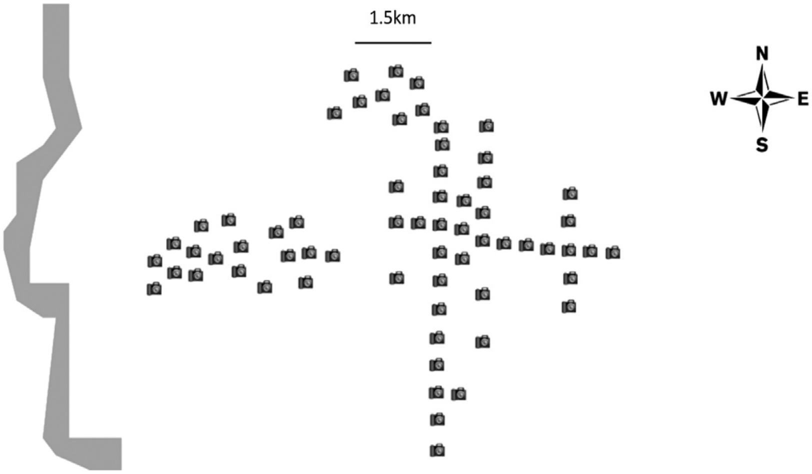

Fig. 4. The grid layout in Bawan.

Table 4
Summary of respondents to questionnaires.

Location	Dates of interviews	Number of respondents	Age range	% of total population	% of male respondents	% of female respondents
Bawan	July–September 2012	77	28–70	4.9	75	25
Belantikan	January–March 2013	20	21–45	0.5	100	0
Kutai	August–October 2012	103	16–63	1.2	60	40
Lesan	NA	NA	NA	NA	NA	NA
Mungku Baru[a]	March–April 2011	20	18–57	0.9	80	20
Murung Raya[a]	July–September 2011	53	16–68	5.0	31	22
Sabangau[a]	April–May 2013	68	28–70	1.3	65	35
Sungai Wain	May–June 2012	12	24–40	0.5	100	0

[a] Data for Mungku Baru, Murung Raya and Sabangau are from Harrison et al. (2010) and Cheyne et al. (2012, 2013) respectively.

et al., 2011; Cheyne et al., 2013) found a good correlation between levels of hunting being reported anecdotally by people and numbers of flying foxes in markets and hunting pressure on clouded leopards in Sabangau; thus we have no reason to suspect that answers were untruthful.

The variables likely to influence attitudes to conservation are listed in Appendix C. We selected respondents from different households and a wide range of different social levels. All questionnaires were carried out in Indonesian. In order to preserve privacy no respondents were photographed while answering questionnaires but the communities were all made aware of the camera trap and questionnaire study at a series of meetings. Informal meetings were held with all villages and village leaders to explain the project. It was made clear no personal information would be used, no photos would be taken and these data were not going to lead to any criminal prosecution. Each individual participant was asked for permission again prior to participating in the questionnaire in case they had not attended the initial socialising meeting. Permissions were also sought from local authorities prior to carrying out the questionnaires. In Sungai Wain the management of the *Hutan Lindung Sungai Wain* (HLSW) refused us permission to carry out structured questionnaires but informal discussions were held with local residents and rangers. In Lesan there were no villages surrounding the forest area.

3.3. Impacts of logging and hunting

A General Linear Model with general contrasts and survey effort as a covariate was carried out to assess the impact of logging and hunting on three variables: total species detected per site (as a % of all detected species), % of carnivores, and % of IUCN concern (Endangered and Vulnerable). Predictors included were: logging status, presence of hunting, habitat type and protected status. All statistical tests were carried out using SPSS v.16, with a significance level of $P < 0.05$. By including survey effort as a covariate this accounts for the wide variation in grids and allows a more comprehensive comparison of the data.

3.4. Occupancy

We used single-season occupancy modelling (MacKenzie et al., 2006) to estimate occupancy probability (Ψ) of taxa at each site. We reconstructed the camera trap history of each species at six sites (Sabangau, Sungai Wain, Kutai, Bawan, Lesan and Belantikan) and divided the data into five-day sampling periods. We did not run occupancy modelling for Mungku Raya and Mungku Baru sites due to lower sample size compared to the other sites. For estimating occupancy of taxa in Sabangau, we took data from the single wet season in 2011–2012 to allow comparison with other sites. Where possible (grids with more than 5 camera stations), we used habitat as covariate. We entered the data into PRESENCE 7.3 (available for free at: www.mbr-pwrc.usgs.gov/software/presence.html). We ranked models based on the Akaike Information Criterion (AIC) values: models with the lowest AIC values were identified as the best output models. All species detected are listed in Appendix A with Occupancy data for each site in Appendix B. A total of 36 mammal species was detected and included in this analysis.

4. Results

1. ***Spatial distribution of mammals***

Occupancy was calculated for all species in all grids and an averaged calculated. (Table 5). Pig-tailed macaques, muntjac, orang-utans, sun bears, bearded pigs and common porcupines consistently had an occupancy of >0.5.

The maximum and minimum distances of detections from forest edge were calculated for each species detection and compared between habitat types. A Mann–Whitney *U*-test was used to assess if there a significant difference in minimum and maximum detection distances between habitats (Table 6).

2. ***Communities, habitat and management structure***

The impacts of forest status, habitat and anthropogenic disturbance were investigated separately due to the wide variation in sample size and types of habitat and disturbance which were represented across the study grids. Additionally, the mammalian community structure, while showing much similarity across study grids, was different, likely as a result of the differences in anthrophonic pressure and natural habitat variation.

4.1. Felid guilds

Only two of the eight grids, Kutai and Lesan, both in East Kalimantan, share the same group of felid species based only on camera trap data. None of the grids has confirmed presence of all five Bornean felids (Table 7 but see discussion). Both the demographics of the individual clouded leopards caught on camera and the numbers of individuals varied from 0 to 3 between grids.

4.2. Impacts of forest status

Camera trap recorded IUCN Red List Endangered mammals at all grids (Table 8).

A General Linear Model with general contrasts and survey effort as a covariate was performed to assess the impact of logging age (number of years since logging occurred), presence of hunting and protected status on each of three variables: total species numbers, % of carnivores, and % of IUCN concern (Endangered and Vulnerable). A Bonferroni correction was applied to the data to correct for multiple comparisons. The model predicted that the age of logging model most consistently explains low species numbers, fewer carnivore species and fewer IUCN E and V species, followed by the presence of hunting model. The protected status model did not explain any of the variation (Table 9).

Table 5
Average detection probability of all mammal species across grids. Due to difficulties in differentiating between greater and lesser mouse deer, yellow and red muntjac and collared and short-tailed mongoose, these species have been combined. See Appendix A for further information.

Species	Average occupancy	Range
Muntjac (combined)	2.30	0.25–5.35
Pig-tailed Macaque	1.80	0.00–5.08
Mouse deer (combined)	1.50	0.15–4.55
Bearded pig	1.00	0.09–2.77
Orangutan	0.66	0.00–0.94
Sun bear	0.61	0.53–0.69
Common porcupine	0.52	0.16–0.85
Malay Civet	0.37	0.00–0.69
Sambar deer	0.30	0.00–0.91
Leopard cat	0.30	0.00–0.65
Clouded leopard	0.27	0.00–0.63
Long-tailed Macaque	0.26	0.00–0.64
Red langur	0.23	0.00–0.53
Yellow-throated Marten	0.16	0.00–0.23
Mongoose (combined)	0.16	0.01–0.38
Common Palm Civet	0.12	0.00–0.59
Banded civet	0.12	0.00–0.36
Pangolin	0.11	0.00–0.19
Long-tailed porcupine	0.10	0.00–0.25
Marbled cat	0.09	0.00–0.19
Flat-headed cat	0.07	0.00–0.28
Banteng	0.06	0.00–0.22
Bay cat	0.06	0.00–0.21
Binturong	0.03	0.00–0.15
Small toothed Palm Civet	0.03	0.00–0.15
Small-clawed otter	0.03	0.00–0.15
Otter civet	0.02	0.00–0.1
Banded Linsang	0.02	0.00–0.1
Moonrat	0.02	0.00–0.1
Horse-tailed squirrel	0.02	0.00–0.1
White-fronted langur	0.02	0.00–0.1
Tarsier	0.01	0.00–0.5
Tufted ground squirrel	0.01	0.00–0.5

Table 6
Relationship between forest edge and minimum and maximum detection distance.

Species	Minimum distance (km)	Maximum distance (km)	Relationship to forest edge
Banteng	$U = 13.47, p = 0.05$	$U = 12.25, p = 0.02$	Detected significantly closer in Lowland Montane.
Bay cat	NS	$U = 5.18, p = 0.04$	Detected significantly farther in Lowland Dipterocarp.
Bearded pig	$U = 9.74, p = 0.05$	$U = 11.32, p = 0.04$	Detected significantly further in Lowland Dipterocarp/PSF and significantly closer in Lowland Montane.
Muntjac	NS	NS	No difference between habitat types.
Clouded leopard	$U = 6.25, p = 0.03$	$U = 9.57, p = 0.02$	Detected significantly further in Lowland Dipterocarp and significantly closer in Lowland Montane.
Flat-headed cat	$U = 8.64, p = 0.04$	NS	Detected significantly closer in Peat-swamp Forest.
Leopard cat	$U = 9.98, p = 0.02$	NS	Detected significantly closer in Peat-swamp Forest.
Marbled cat	$U = 14.43, p = 0.02$	$U = 9.24, p = 0.01$	Detected significantly closer in Peat-swamp Forest and Lowland Montane.
Mouse deer	NS	NS	No difference between habitat types.
Sambar deer	$U = 8.25, p = 0.01$	NS	Detected significantly closer in Peat-swamp Forest.
Sun bear	NS	NS	No difference between habitat types.

4.3. Impacts of habitat

A General Linear Model with general contrasts and survey effort as a covariate was performed to assess the impact of burnt areas in the forest, habitat type and elevation on each of three variables: total species numbers, % of carnivores, and % of IUCN concern (Endangered and Vulnerable). The model predicted that the presence of burnt areas most consistently explains low species numbers and fewer carnivore species but not fewer IUCN E and V species. The habitat type and elevation models did not explain any of the variation (Table 10).

3. ***Anthropogenic disturbance***

We compared mammalian species assemblages between forests with different human impacts and distance from human settlements (Table 11).

Table 7
Distribution of felid species and demographics across all grids as detected by the cameras (number of independent photos) X = not detected.

Grid	Clouded leopard	Leopard cat	Flat-headed cat	Marbled cat	Bay cat	Total felid species	Total males	Total females	Total unknown	Total
Bawan	X	1	X	1	X	2	0	0	0	0
Belantikan	3	3	X	X	X	2	1	0	0	1
Kutai	1	1	X	1	2	4	1	0	0	1
Lesan	3	2	X	1	1	4	2	0	1	3
Mungku Baru	1	1	X	X	X	2	0	1	0	1
Murung Raya	1	1	X	1	X	3	0	0	1	1
Sabangau[a]	152	74	30	41	X	4	4 (8)	1 (1)	0 (0)	4 (9)
Sungai Wain	12	1	1	X	1	4	2	0	0	2

[a] Sabangau data are from the 6-month comparison survey period, data in brackets are numbers from the full 7 years of survey (Adul et al., 2015).

Table 8
Distribution of IUCN status species across all grids.

Grid	Logging status/age	Hunting	Total species	E	V	NT	LC	DD
Bawan	Current	Y	19	1	3	0	15	0
Belantikan	>20	Y	30	3	8	1	18	0
Kutai	>10	Y	27	4	5	0	18	0
Lesan	>20	Y	29	3	7	0	19	0
Mungku Baru	>20	Y	21	4	8	2	7	0
Murung Raya	NA	Y	10	0	7	0	3	0
Sabangau	>10	Y	32	5	7	0	20	0
Sungai Wain	>20	N	30	6	6	0	18	0

Table 9
GLM results for logging, hunting and protected status.

Variables in the model	Age of logging	Presence of hunting	Protected status
Total species numbers	$F = 6.3, p = 0.012$*	$F = 5.4, p = 0.033$*	$F = 8.4, p = 0.080$
% of carnivores	$F = 1.5, p = 0.021$*	$F = 4.8, p = 0.041$*	$F = 5.9, p = 0.200$
% of IUCN concern	$F = 5.9, p = 0.044$*	$F = 5.0, p = 0.044$*	$F = 6.0, p = 0.310$

* Significant results.

Table 10
GLM results for presence of burnt areas, habitat type and elevation.

	Presence of burnt areas	Habitat type	Elevation
Total species numbers	$F = 5.3, p = 0.018$*	$F = 5.7, p = 0.080$	$F = 5.8, p = 0.070$
% of carnivores	$F = 6.8, p = 0.023$*	$F = 6.8, p = 0.100$	$F = 6.7, p = 0.090$
% of IUCN concern	$F = 7.0, p = 0.060$	$F = 7.1, p = 0.120$	$F = 8.8, p = 0.100$

* Significant results.

Table 11
Details of minimum distances to disturbance for each grid.

GRID	Distance to tarmac road (km)	Distance to dirt road (km)	Distance to village (km)	Distance to river (km)	Presence of logging camp in forest
Bawan	7.1	0.5	7.2	8.4	N
Belantikan	5.6	0.2	1	2	N
Kutai	13	0.5	3.5	1.5	N
Lesan	6.3	2	3.8	2.4	N
Mungku Baru	4	4	2	0.3	N
Murung Raya	45	15	10	0.1	N
Sabangau	4	4	6	1.5	N
Sungai Wain	6.7	2.4	6	1	N

A General Linear Model with general contrasts and survey effort as a covariate was performed to assess the impact of distance to tarmac road, distance to dirt road, distance to village, distance to river and presence of logging camp in the forest on each of three variables: total species numbers, % of carnivores, and % of IUCN concern (Endangered and Vulnerable). None of these models explained the variation in total species numbers, % of carnivores, and % of IUCN concern (Endangered and Vulnerable).

Fig. 5. Leopard cat skin in a family home. The cat was trapped and killed as it was believed to be consuming chickens. Photo taken in Tumbang Tujang village, Murung Raya District (central highlands) by BRINCC Expedition team in 2011 (Cheyne et al., 2012).

4.4. Hunting

Species which were regularly hunted were deer (muntjac, mouse and sambar—average 40% of respondents), bearded pigs (20%) and pangolins (8%). Guns and spears were more commonly used than snares. Recognition and correct identification of photos of clouded leopards varied from 34%–68% of respondents. Incorrect answers were leopard cat, tiger and lion. Only in Kutai and Murung Raya was it reported that cats were hunted for their skin (Fig. 5).

5. Discussion

We have shown how different types of forest disturbance affects the species variation in mammal communities. The variation in the guild of mammals present in an area can be used as an indicator of disturbance.

1. ***Spatial distribution of mammals***

Pig-tailed macaques, muntjac, orang-utans, sun bears, bearded pigs and common porcupines consistently had an occupancy of >0.5 suggesting that these species are using all surveyed areas of the forest irrespective of disturbance levels or habitat type. Likely due to the high levels of terrestriality and generalist diet, the pig-tailed macaques were the most frequently detected species combined across all grids followed by bearded pigs, sun bears, orang-utans (Ancrenaz et al., 2014) and muntjac species.

Even within the most disturbed forest (Bawan) these large mammals were making use of the forest edge. Bearded pigs were generally found close to the forest edge but ranged further into the forest interior in LD, LD/PSF and PSF. Clouded leopards, leopard cats and marbled cats were all found <1 km from the forest edge only in PSF. Sambar deer were found <2 km from the forest edge only in Lowland Montane.

2. ***Communities, habitats and management strategy***

5.1. Felid species guilds

While difficult to confirm absence based only on camera trapping, some clear relationships emerge from the data: Clouded leopards were always found in forest with sambar deer (possible prey) and flat-headed cats are never found in forest without otter civets and Storm's storks. Both otter civets and sambar deer were found at low occupancy thus communities could be determined by habitat specific species (e.g. wetland specialists) or by less common species e.g. sambar deer rather than muntjac, mouse deer or bearded pigs. With regard to the felids, the following relationships are emerging:

- If clouded leopards were present, there were also leopard cats and marbled cats.
- If flat-headed cats were present, there were also clouded leopards, leopard cats and marbled cats.
- If bay cats were present there were also clouded leopards, leopard cats and marbled cats.
- None of the grids has confirmed presence of all five Bornean felids despite camera trapping continuously for 90–180 days.

Elsewhere on Borneo all five felids do co-occur. Sungai Wain is suspected to support all five species but the marbled cat was not detected in this study. Murung Raya is also likely to support all five felids. The flat-headed cat is a habitat-restricted species requiring wetlands (Wilting et al., 2010, 2016) and the bay cat has never been recorded in peat-swamp forest (Sastramidjaja et al., 2015) thus absence of these cats is not necessarily related to habitat disturbance.

Female clouded leopards had lower encounter rates than males with only 2 females being captured during the study at different grids compared to 14 males. It is clear that there is a bias in the sex of detected clouded leopards at all grids (7:1 in Sabangau). This study demonstrates the challenge with surveying clouded leopard populations where sample sizes are small, which is often the norm for rare carnivore studies, thus reliable density estimates are hard to obtain. Cheyne et al. (2013) propose several hypotheses as to the low capture rate of females in peat-swamp forest. With the benefit of more survey grids and habitat types, these hypotheses remain plausible. Females are smaller than males and probably have sole responsibility for raising cubs; therefore, our current hypotheses as to the lack of photo detections of females are as follows.

(1) Females were not detected on any trails. We strongly suspect that the females are staying well away from any human disturbance thus they are avoiding trails or they are avoiding trails because they are avoiding people. (2) Females were not photographed on any cameras which also captured males. (3) Females are staying away from high concentrations of males as they cannot compete for prey with so many larger males present. (4) All study grids are in selectively logged/disturbed forest. This may render these areas unsuitable for denning cubs so the females do not come there. It is worth noting that the grids with the highest number of encounters with (male) clouded leopards were grids with long-term trails established for at least 10 years, thus perhaps the clouded leopards become tolerant of long-term human presence as long as they are not being persecuted. (5) Sollmann et al. (2011) point out that in other pantherine species, male cats move over larger areas than females and are perhaps more readily detected by camera traps. (6) Wilting et al. (2012) highlight that female clouded leopards may also spend more time in trees than males as they may be more agile and better climbers due to their lower body weight, thus females may be detected less often on ground-based camera traps.

5.2. Forest status

Camera trapping recorded IUCN Red List Endangered mammals at all grids. Age of logging and hunting pressure were negative indicators of species numbers, % of carnivores and % of IUCN Endangered and Vulnerable species. The two variables are correlated as opening an area for logging often leads to increased human activity. Different species will respond to pressures differently and species will be impacted by hunting pressure in different ways e.g. species targeted for food or retribution will be more heavily impacted. The protected status of the forests did not significantly predict species numbers, % of carnivores and % of IUCN species, perhaps due to the fact that few protected areas have reliable and effective patrol teams thus human impacts on forests are consistent across protected area status.

5.3. Habitat type

Only the presence of burnt areas was found to significantly affect the total number of species and the % of carnivore species in an area. Elevation was not a predictor of any of the variables, likely due to the small variation in elevation from ∼10–350 m a.s.l. Montane areas lack surveys due to inaccessibility but these areas require more work (Geise et al., 2004; Glessner and Britt, 2005; Jennings et al., 2013). Habitat type again was not a significant predictor of species numbers, % of carnivores or % of IUCN species overall though some specialists do have habitat preferences e.g. flat-headed cats and otter civets preferring wetlands and banteng and bay cats apparently avoiding PSF.

3. ***Anthropogenic disturbance***

The presence of indirect infrastructure did not significantly impact the community structure or presence. The age of indirect logging and direct hunting presence significantly impacted total species richness, % of species that were carnivores, and % of species of IUCN concern (Endangered and Vulnerable). Hunting will be of greater conservation threat for some species than others e.g. primates and ungulates. Logging is more likely to impact other larger mammals e.g. felids, sun bears and sambar deer (Meijaard et al., 2005). While none of the cat species was reported as being hunted, hunting of these cats does occur.

4. ***Using mammal communities as indicators of human perturbation***

Ecological indicators of habitat quality are a valuable tool for conservation biologists. Previous explorations of indicator performance have generally focussed on single species. Species selection has been based on (1) ease of survey, (2) ease of identification and (3) life history traits, e.g. short-lived species are favoured based on the assumption that they will respond faster to change. Although indicators based on individual species can be useful for developing support for a monitoring program or evoking a public response to an environmental issue, the reliability of individual species as indicators can be problematic if precise estimates are difficult to achieve due to issues with measurement, or if there is considerable natural variation in the real numbers and distribution of a species (Harrison et al., 2005, 2012a; Gardner, 2010). Variation in numbers and distribution can be caused by many factors including natural population cycles, seasonality, sampling error, annual movements, and natural variation in response to habitat structure.

The use of focal or indicator species has been questioned (Van Horne, 1983; Pearson, 1994; Carignan and Villard, 2001; Harrison et al., 2012a). An alternative approach is to combine a number of ecological attributes into a holistic assessment of the state of the ecosystem, given that no one species is likely to provide a complete picture of ecosystem integrity (Cushman and McGarigal, 2003). Single elements often show sensitivity to different factors e.g. human influence. The use of communities as functional groups of indicators may be a more promising option but needs further work (Dufrêne and Legendre, 1997; Bayne et al., 2004; Cushman et al., 2009). Diversity measures such as species richness are often proposed as ecological indicators because of their reduced variability compared with abundance.

We sought to determine the value of using indicator communities' i.e. large and/or small mammals, rather than focusing on life history of individual species, both to evaluate the effectiveness of this approach and as an alternative to using skilled botanists who are often in short supply. Camera trapping at this scale is both expensive and time-consuming, and for some of these species, such as most felids, sample sizes thwart accurate density analysis (Gordon and Stewart, 2007; Wilting et al., 2010, 2012; Brodie and Giordano, 2012; Cheyne et al., 2013), however, combining these data with those for the wider mammal guild is useful.

6. Conclusions

The history of logging, the presence of hunting of burnt forest emerge strongly as significantly negatively associated with mammalian community diversity. While the infrastructure changes were not statistically significant, it is perhaps too soon to determine if roads, logging camps and tracks to have an impact or not. The size of the forest will likely affect the mammal communities; more work is needed on small fragments to compare persisting mammalian guilds with larger landscapes. We have demonstrated that wide and disparate datasets can provide ecological monitoring value and urge for more investigation into the use of community and guild datasets as well as the long-term impacts of infrastructure development. We have identified 4 species as specific indicators whose presence or absence can help determine the type and/or extent of forest disturbance and/or be a proxy indicator for the presence of other species. Leopard cat (*Prionailurus bengalensis*) and pig-tailed macaques (*Macaca nemestrina*, generalists); sambar deer (*Rusa unicolour*, large, wide-ranging herbivores) and clouded leopards (*Neofelis diardi*) as a proxy for at least 2 of the smaller felid species. We propose that it is the presence of generalist and rare/specialist species which could be a good measure of the level of ecosystem disturbance as well as the completeness of the whole mammalian community.

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Appendix A

Species	Scientific name	Order	IUCN status	Number of trap days with >1 detection
Banded civet	*Hemigalus derbyanus*	Carnivora	V	29
Banded Linsang	*Prionodon linsang*	Carnivora	LC	7
Banteng	*Bos javanicus*	Cetartiodactyla	E	17
Bay cat	*Pardofelis badia*	Carnivora	E	3
Bearded Pig	*Sus barbatus*	Cetartiodactyla	V	752
Binturong	*Arctictis binturong*	Carnivora	V	2
Clouded Leopard	*Neofelis diardi*	Carnivora	V	162
Common Palm Civet	*Paradoxurus hermaphroditus*	Carnivora	LC	5
Common porcupine	*Hystrix brachyura*	Rodentia	LC	192
Flat-headed Cat	*Prionailurus planiceps*	Carnivora	E	32
Horse-tailed Squirrel	*Sundasciurus hippurus*	Rodentia	NT	1
Leopard Cat	*Prionailurus bengalensis*	Carnivora	LC	78
Long-tailed Macaque	*Macaca fascicularis*	Primates	LC	68
Long-tailed porcupine	*Trichys fasciculata*	Rodentia	LC	11
Malay Civet	*Viverra tangalunga*	Carnivora	LC	85
Marbled Cat	*Pardofelis marmorata*	Carnivora	V	27
Mongoose (combined)	*Herpestes brachyurus* and *Herpestes semitorquatus*	Carnivora	LC	113
Moonrat	*Echinosorex gymnura*	Insectivora	LC	15
Mouse Deer (combined)	*Tragulus kanchil* and *Tragulus napu*	Cetartiodactyla	LC	316
Muntjac (combined)	*Muntiacus muntjak* and *Muntiacus atherodes*	Cetartiodactyla	LC	553
Orangutan	*Pongo pygmaeus*	Primates	E	142
Otter Civet	*Cynogale bennettii*	Carnivora	E	7
Pangolin	*Manis javanica*	Pholidota	E	20
Pig-tailed Macaque	*Macaca nemestrina*	Primates	V	2635
Red langur	*Presbytis rubicunda*	Primates	LC	35
Sambar Deer	*Rusa unicolour*	Cetartiodactyla	V	87
Small toothed Palm Civet	*Arctogalidia trivirgata*	Carnivora	LC	4
Small-clawed Otter	*Aonyx cinerea*	Carnivora	V	3
Sun Bear	*Helarctos malayanus*	Carnivora	V	653
Tufted ground squirrel	*Rheithrosciurus macrotis*	Rodentia	V	3
White-fronted langur	*Presbytis frontata*	Primates	V	4
Yellow-throated Marten	*Martes flavigula*	Carnivora	LC	26

Appendix B. Occupancy for all grids

Species	Bawan		Belantikan		Kutai		Lesan		Sabangau		Sungai Wain	
	Ψ	P	Ψ	P	Ψ	P	Ψ	P	Ψ	P	Ψ	P
Banded civet	–	–	0.11	0.30	–	–	0.24	0.08	–	–	0.36	0.15
Banded Linsang	–	–	–	–	–	–	–	–	0.10	0.70	–	–
Banteng	–	–	0.13	0.08	0.22	0.05	–	–	–	–	–	–
Bay cat	–	–	–	–	0.12	0.01	–	–	–	–	0.21	0.80
Bearded Pig	0.16	0.11	0.69	0.29	0.64	0.43	1.00	0.34	0.59	0.25	0.48	0.53
Binturong	–	–	0.02	0.60	–	–	–	–	0.15	0.90	–	–
Clouded Leopard	–	–	0.27	0.40	0.46	0.30	–	–	0.63	0.20	0.26	0.30
Common Palm Civet	–	–	–	–	0.59	0.40	–	–	0.15	0.40	–	–
Common porcupine	0.16	0.45	0.73	0.30	0.85	0.40	0.48	0.20	0.40	0.80	0.51	0.30
Flat-headed Cat	–	–	–	–	–	–	–	–	0.12	0.04	0.28	0.03
Horse-tailed Squirrel	–	–	0.10	0.60	–	–	–	–	–	–	–	–

Species	Bawan		Belantikan		Kutai		Lesan		Sabangau		Sungai Wain	
	Ψ	*P*	*Ψ*	*P*	*Ψ*	*P*	*Ψ*	*P*	*Ψ*	*P*	*Ψ*	*P*
Leopard Cat	0.61	0.30	0.65	0.30	–	–	–	–	0.51	0.40	–	–
Long-tailed Macaque	0.33	0.04	0.45	0.40	–	–	–	–	0.16	0.70	0.64	0.20
Long-tailed porcupine	–	–	0.18	0.70	0.19	0.60	–	–	–	–	0.25	0.40
Malay Civet	–	–	0.20	0.20	0.50	0.50	0.23	0.40	0.57	0.30	0.69	0.40
Marbled Cat	0.16	0.20	–	–	0.19	0.20	–	–	0.18	0.20	–	–
Mongoose (combined)	0.10	0.10	0.01	0.70	0.10	0.30	0.18	0.40	0.38	0.30	0.17	0.40
Moonrat	–	–	–	–	–	–	–	–	0.10	0.80	–	–
Mouse deer (combined)	0.16	0.04	0.23	0.03	0.87	0.11	0.33	0.19	0.43	0.04	0.32	0.08
Muntjac (combined)	0.62	0.06	0.58	0.11	0.59	0.23	0.85	0.24	1.00	0.05	0.68	0.20
Orangutan	0.77	0.04	0.80	0.03	0.88	0.08	0.56	0.20	0.94	0.02	–	–
Otter Civet	–	–	–	–	–		–	–	0.04	0.30	0.10	0.60
Pangolin	–	–	–	–	0.19	0.80	0.16	0.70	0.16	0.60	0.12	0.80
Pig-tailed Macaque	0.38	0.07	1.00	0.02	0.63	0.18	0.82	0.10	1.00	0.05	0.78	0.23
Red langur	0.23	0.04	–	–	–	–	–	–	0.53	0.04	–	–
Sambar deer	–	–	0.51	0.08	0.11	0.24	0.54	0.02	0.13	0.34	0.67	0.01
Small toothed Palm Civet	–	–	–	–	–	–	–	–	0.15	0.70	–	–
Small-clawed Otter	–	–	–	–	–	–	–		0.15	0.70	–	–
Sun bear	0.66	0.03	0.53	0.03	0.55	0.04	0.61	0.05	0.62	0.02	0.69	0.03
Tarsier	–	–	–		–	–	–	–	0.05	0.80	–	–
Tufted ground squirrel	–		0.05	0.70	–	–	–	–	–	–	–	–
White-fronted langur	–		0.10	0.60	–	–	–	–	–	–	–	–
Yellow-throated Marten	0.23	0.03	0.17	0.10	0.19	0.20	0.16	0.50	0.21	0.50	–	–

Appendix C

Independent variables	*Categories*
Marital status	Yes, No, Widowed
Education	SD, SMP, SMA, D1, D3, S1, STM
Employment	Unclear, Private, State, Housewife, Farmer, Teacher, Retired, Boat maker, Driver, Shop owner, Miner, Unemployed, Student
Ethnicity	Unclear, Dayak, Javanese, Banjar, Bugis, Flores, Sulteng, Balinese, Toraja, Timur, Buthon, Sangir, Gorontalo, Batak
Religion	Muslim, Protestant, Catholic, Kaharingan, Budhist
Frequency visiting the forest	Never, Hardly ever, Every week, Every month, Irregular, Daily
Purpose of forest visit	None, Shortcut, Stroll, Medicinal plants, Fishing, Hunting, Rotan/bambu, Live animals, Check land, Firewood, Fruit, Damar, Guide researchers/guests, Seedlings for crop, Survey for coal company, Vegetables
Most feared animal in the forest	Nothing, Crocodile, Sun bear, Clouded leopard, Orangutan, Python, Pig-tailed macaque, Tiger, All, Other
What will happen if there is no more forest	More fires, More floods, More insects, Less problems with animals, More landslides, More pollution, Less clean water, Do not know, Animals leave the forest, Turn into plantation, Increased temperature, Tame the animals, Loss of plant material (firewood, medicinal plants and fruits), Extinction of animals, More difficult to hunt and fish

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