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Habitat use and predicted range for the mainland clouded leopard *Neofelis nebulosa* in Peninsular Malaysia

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ABSTRACT

Ongoing deforestation in Southeast Asia is leading to increased fragmentation and reduction of habitat for the mainland clouded leopard (*Neofelis nebulosa*). Using the largest detection/non-detection camera trap survey dataset known for the species throughout its range, we investigated factors affecting clouded leopard habitat use across Peninsular Malaysia. Habitat use was modelled using fine scale covariates and recently developed analytical techniques to account for spatial autocorrelation. Clouded leopard habitat use increased with increasing distance from water bodies, higher numbers of discontinuous core areas per unit area and higher elevation. In addition, clouded leopard habitat use was higher in sites with higher average forest change values. After extrapolating the predicted habitat use of clouded leopards across the whole of Peninsular Malaysia, we assessed the suitability of proposed ecological linkages, and identified other suitable forest patches not within the current Central Forest Spine. Our findings are valuable for land use planning and management, in particular, for determining the suitability of forest remnants to support populations of clouded leopard and predicting how this species will respond in human-dominated landscapes.

1. Introduction

Deforestation across Southeast Asia has contributed to the collapse of large carnivore ranges (e.g. Rostro-Garcia et al., 2016). In Malaysia, continued depletion and fragmentation of tropical rainforests (e.g. by roads and logging; Clements et al., 2014; Rayan & Linkie, 2015) have placed many carnivore species under heavy pressure (e.g. Hedges et al., 2013; Wadey et al., 2014). Peninsular Malaysia has experienced drastic and rapid forest loss; at the turn of the 19th century forest coverage was at 90%, but by 2012 only 38–45% forest coverage remained (DTCP, 2009; Miettinen et al., 2011). Cleared areas have been largely converted to agriculture, plantation forest or settlements. In 2009, the Central Forest Spine (CFS) Master Plan for Ecological Linkages was created as a government initiative to protect biodiversity and ecosystem services by securing connectivity between Peninsular Malaysia's forest blocks. It covers an area of approximately 5.3 million ha and over 91% of the forests in Peninsular Malaysia. However, there still remains 4.2 million ha of unprotected forest in the CFS and most of the linkages have not attained protected area status and some continue to experience fragmentation (DTCP, 2009; Clements, 2013; Jain et al., 2014). Further, some of the linkages have been completely lost due to development or establishment of plantations (Jain et al., 2014). It is

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thus increasingly pertinent to understand which aspects of the landscape affect the persistence of large carnivores and in turn assess the suitability of these ecological linkages for these species.

The mainland clouded leopard (*Neofelis nebulosa*) is a carnivore that inhabits forested landscapes of Asia. It is a medium-sized felid (11–23 kg) with a patchy distribution that ranges from Nepal and southern China to Peninsular Malaysia in the South (Grassman et al., 2015). Categorized as Vulnerable on the IUCN Red List of Threatened Species, the main local threats to its persistence include habitat loss due to deforestation for agriculture (oil palm and rubber; Aziz et al., 2010; Koh and Wilcove, 2008) and hunting (Nowak, 2005; Oswell, 2010). Clouded leopards are known to be secretive, solitary, primarily nocturnal/crepuscular animals that usually occur at naturally low densities (Grassman et al., 2005; Rao et al., 2005). The species has been recorded at altitudes up to 2500 m asl and it is thought to prefer closed forest over more open habitats (Austin et al., 2007; but see Hedges, 2014). Clouded leopards have been recorded in a variety of habitats, mainly primary, secondary and selectively logged forests, and a minority of occurrences in degraded dry woodlands, grassland, scrub and mangrove swamps (Dinerstein & Mehta, 1988; Nowell & Jackson, 1996; Mohamad et al., 2015). There is limited information on the clouded leopard's home range: two studies in Thailand estimated it to be about 30–40 km^2, with substantial overlap between and within sexes (Grassman et al., 2005; Austin et al., 2007). In Malaysia, density estimates vary from 1.8 to 4.7 clouded leopards per 100 km^2 (Hedges, 2014; Mohamad et al., 2015). Clouded leopard habitat use in Peninsular Malaysia was found to be highly influenced by the availability of small and medium prey species (<10 kg; Mohamad et al., 2015). The study therefore highlighted the conservation importance of species such as pig-tailed macaques, porcupine, mouse deer and small carnivores to enable clouded leopards to viably persist (Mohamad et al., 2015). Notwithstanding these fragments of knowledge on the clouded leopard, little is known of the determinants of habitat suitability for the species (Austin et al., 2007; Mohamad et al., 2015).

Understanding the spatial ecology of elusive, forest dwelling carnivores such as the clouded leopard that occur at naturally low densities, remains challenging (Sunarto et al., 2013). Modelling habitat use using occupancy models, which explicitly account for imperfect detection during surveys and enables the analysis of how different covariates affect it (MacKenzie et al., 2002; Thompson, 2004), is particularly important for these kinds of studies. One assumption of habitat use modelling is the closure between surveys, whereby there is no change in habitat use intensity between surveys (MacKenzie et al., 2002). Another assumption for estimating habitat use is that the detection of the species at a site is independent of detecting the species at any other sites (MacKenzie et al., 2002). However, this assumption may not be valid, especially for transect surveys or dense sampling unit layouts. To resolve the lack of independence between survey units, we utilized a hierarchical spatial occupancy model with a probit mixture framework to resolve the lack of independence and minimize spatial confounds whilst improving algorithm convergence (Johnson et al., 2013). This statistical method has also been proposed to be particularly effective over large spatial extents, as in the case of our study which combines multiple camera-trap surveys distributed across Peninsular Malaysia. Therefore, we employed this approach to account for spatial autocorrelation, and compared the results with models not taking into account the possible interdependence of detection rates within neighboring sites.

The aim of this study is to investigate factors that affect the habitat use of the mainland clouded leopard on a regional scale across Peninsular Malaysia. Specifically, our objectives are to (1) identify key environmental variables and examine their influence on its use of habitat, (2) predict the habitat use intensity of the clouded leopard across Peninsular Malaysia and (3) critically assess the protective coverage of the CFS and its linkages for this species. We do this by using detection/non-detection data from nine camera-trap surveys in Peninsular Malaysia, which when combined constitute the largest known dataset so far explored for the species. We analyze habitat use using a occupancy modelling framework, accounting for spatial autocorrelation in the dataset (Johnson et al., 2013). Finally, we use the best model to extrapolate the predicted habitat use across Peninsular Malaysia and compare this with the boundaries of CFS areas and linkages.

2. Methods

2.1. Study areas

Records of clouded leopard from nine camera trap surveys across Peninsular Malaysia conducted between 2009 and 2015 (Fig. 1) were included in the analysis. In chronological order, the survey sites were located at Temengor Forest Reserve, western region of Taman Negara National Park, Royal Belum State Park, 'Primary Linkage 7' (DTCP, 2009) in eastern Peninsular Malaysia, 'Primary Linkage 8' (DTCP, 2009) in western Peninsular Malaysia, Pasoh Forest Reserve and Ulu Muda Forest Reserve. Supplementary Methods S1 provides more details on the surveys. Table 1 depicts a summary of the mean number of days the stations were deployed for, the number of stations, effort, mean trap spacing and total number of records of clouded leopards.

The vegetation on all the surveyed sites predominantly consists of lowland-hill or upper-hill dipterocarp forest, as well as montane forest. All the survey sites, with the exception of Royal Belum State Park and Taman Negara, had been selectively logged between 1970 and now.

2.2. Analysis

Clouded leopard detection histories for each survey were developed based on the photographic records (where 1 represents that the species was detected at a specific camera-trap station on a specific day, and a 0 represents no detection). Only the first 120 days of each camera trap station were included in the analysis in order to minimize the risk of violating the closure assumption when estimating habitat use (Rota et al., 2009). Further, only two of nine surveys had >120 days of deployment (Table 1). The 120-day data subset was collapsed into multiple-days sampling occasions. The goodness of fit of the most complex model (global model) that included all contributing covariate was tested in four different collapsing scenarios (7, 10, 12 and 15-day period; MacKenzie & Bailey, 2004). The 15-day period represented the optimum period length to maximize model fit (Table S1). Collapsing of sampling periods increased temporal independence among occasions and overall detection probability, which if too low can prevent model convergence (Otis et al., 1978; Dillon & Kelly, 2007). The collapsed detection histories for each site were combined into one data matrix.

Based on past studies (Clements, 2013; Hedges, 2014; Mohamad et al., 2015), seven site covariates considered to be potentially influential for clouded leopard habitat use were modelled: Elevation (ELEVATION), distance to river or stream (DRAINAGE), distance to lakes edge (LAKE), distance to road (ROAD), distance to nearest town or village (VILLAGE), forest cover (VCF, GFC30, GFC50, GFC75, GFC90; see below for elaboration), and measures of forest fragmentation (DCAD, CWED, CONTIG; see below for elaboration). Specifically, clouded leopard habitat use can be affected by covariates that reflect human activity and fragmentation, either in a negative (e.g. road; Clements, 2013) or a positive manner (e.g. clear felling; Hedges, 2014). Positive associations were expected with elevation (Haidir et al., 2013) as this could be a distal factor that likely influences prey availability (Mohamad et al., 2015). Moreover, because of the reputed arboreal habit of the clouded leopard (Rabinowitz et al., 1987; Nowell & Jackson, 1996), the species was also expected to be associated with closed forest cover (Austin et al., 2007; Brodie & Giordano, 2012). Thought to be most strongly associated with primary forest (Hunter, 2011), recent evidence indicated that forest type (whether primary or selectively logged) might not be an important determinant of its presence (Mohamad et al., 2015). Probability of detection was assessed in relation to two survey covariates: the

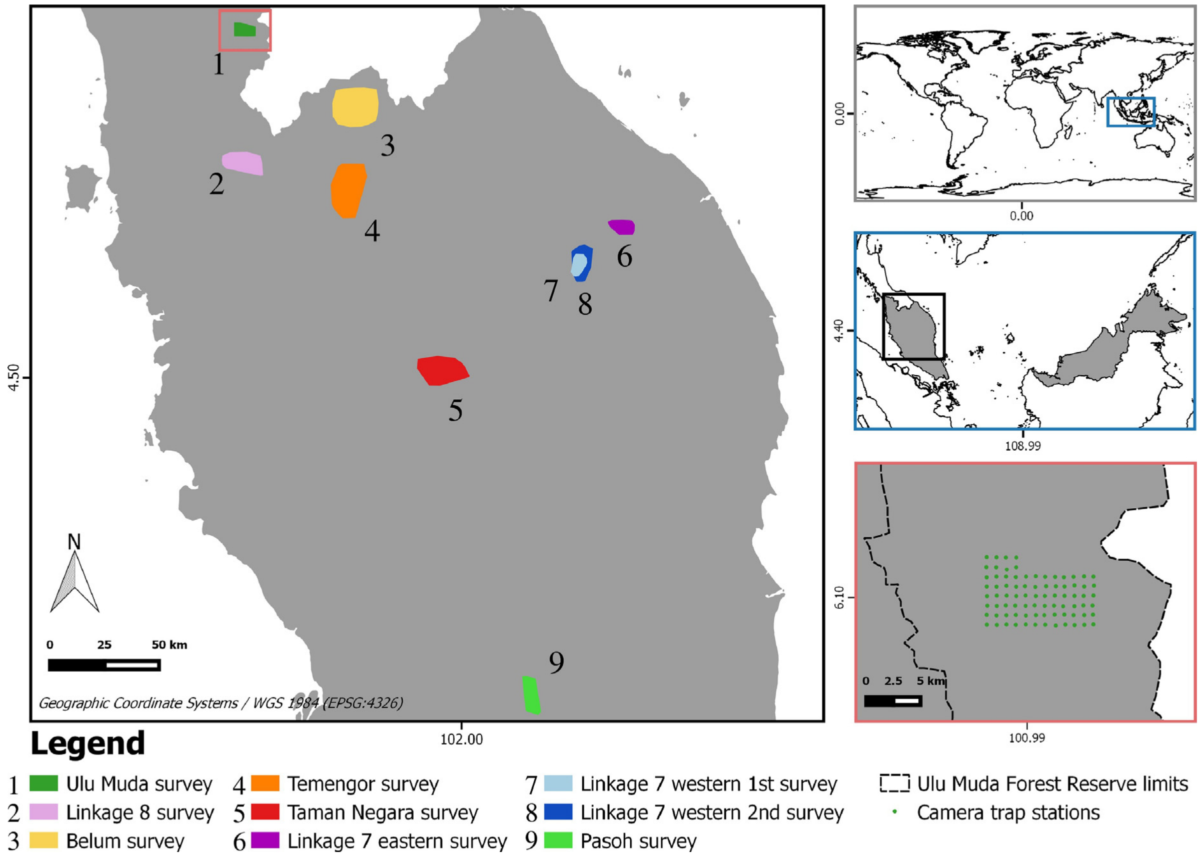

Fig. 1. Map with the camera-trap surveyed areas (sites) used to model mainland clouded leopard (*Neofelis nebulosa*) habitat use in the Peninsula Malaysia. Projection: UTM 47 N, Datum: WGS 1984 (EPSG32647).

surveyed area (SITE), and number of days a camera-trap station was active for during each sampling occasion (EFFORT). Sites 7 and 8 (Fig. 1) were treated as one study area.

Site covariates were generated using Quantum GIS (QGIS) version 2.6.1 (QGIS Development Team, 2014). For all covariates, the value was the mean of all raster cells included in a 500 m radius around each camera-trap station. The radius was established to represent the peripheral area around the camera-trap stations, minimizing overlap between neighboring stations (mean spacing between neighboring camera-trap stations was 1090 m). The source of each covariate is described in Methods S1. The Global Forest Change (GFC, Hansen et al., 2013) layer allows the user to set a threshold of percentage tree cover that is to be considered as forest. Without any auxiliary data or field verification, assigning the threshold values to GFC is subjective (Tropek et al., 2013). For that reason, four different threshold values (30, 50, 75 and 90%) were tested for their effects on the intensity of clouded leopard habitat use. Where it was not possible to find VCF and GFC maps specific for the year of the survey, we used maps from the most recent years (e.g. the latest VCF and GFC maps are for 2010 and 2012, respectively). Disjunct Core Area Density (DCAD) is the number of disconnected patches of suitable interior habitat per unit area. Because different locations experienced different degrees of logging (see above on surveys), DCAD was chosen to represent the varying number of disjunct patches across sites. Contrast-weighted edge density (CWED) is a measure of edge density standardized to a per unit area and was selected to understand the effects of edge on clouded leopard habitat use. Contiguity index (CONTIG) is an index of spatial connectedness of forest and was selected to examine whether clouded leopard preferred a contiguous forest cover (for details refer to Fragstats' help manual; McGarigal, 2014).

Pearson's correlation test was used to identify collinearity between all continuous site covariates. Any combination of covariates with $r > |0.6|$ was considered correlated and the covariate that performed better in the univariate habitat use models was retained. Prior to the

Table 1
Details of camera trap survey for mainland clouded leopard in Peninsular Malaysia. Effort is total number of days for which camera traps were active at that site, spacing between station is in meters.

Year	Site	Mean no. of days deployed (SE)	Stations	Effort	Spacing in m (SD)	Records of clouded leopards
2009–2010	Temengor Forest Reserve	92.2 (54.2)	175	16,143	851.9 (432.3)	120
2010–2011	Taman Negara National Park	142.6 (100.2)	36	5170	1776.0 (973.1)	40
2010–2011	Royal Belum State Park	102.5 (61.7)	175	17,936	1041.0 (897.0)	116
2011–2012	Primary Linkage 7* (eastern block)	67.1 (9.0)	81	5437	736.0 (182.7)	59
2012–2013	Primary Linkage 7* (western block)	65.8 (5.7)	77	5065	733.1 (199.9)	14
2012–2013	Primary Linkage 8*	61.4 (5.4)	182	11,176	772.3 (149.1)	70
2013	Pasoh Forest Reserve	24.3 (7.9)	55	1334	1268.9 (199.8)	1
2013	Primary Linkage 7 (western block)	174.3 (14.0)	62	10,809	1390.5 (262.8)	46
2014–2015	Ulu Muda Forest Reserve	119.1 (38.9)	80	9531	933.2 (49.5)	11
	Total		923	82,601		477

* Consists of Forest Reserves.

Table 2
Clouded leopard detection probability (p) models. AIC_c akaike's information criterion corrected for finite sample sizes. ΔAIC_c relative difference in AIC_c values compared with the top ranked model, AIC_cwt weight, K number of parameters.

	AIC_c	ΔAIC_c	AIC_cwt	K	−2 log likelihood
p (site + effort)	2392.45	0	1.00	10	1186.23
p (effort)	2413.78	21.33	0.00	3	1203.89
p (site)	2442.59	50.14	0.00	9	1212.30
p (·)	2458.77	66.32	0.00	2	1227.40

modelling, all continuous covariates were standardized to z-scores $[(y - \bar{y})/SD]$ to facilitate use of a numerical optimisation algorithm and prevent failure in the parameter estimation (Donovan & Hines, 2007).

Modelling was conducted in three phases: multivariate modelling without spatial autocorrelation, multivariate modelling with spatial autocorrelation, predictive mapping of distribution. As we had a large number of covariates, our phase-wise approach enabled the selection of important covariates for subsequent steps. In the first phase, the most informative covariates were selected using single-species, single-season habitat use models in the R package “unmarked” version 0.10–6 (Fiske and Richard, 2011) in R 3.1.2 (R Core Team, 2014). We modelled detection probability (p) by allowing the habitat use parameter to remain constant or to vary with individual or additively combined detection covariates. The significant contributing detection covariates were retained and used to model habitat use probability in relation to the site covariates (Long et al., 2011). Subsequently, models with all possible combinations of uncorrelated site covariates were compared. Covariates considered to have a strong influence on habitat use were those that attained summed model weights (importance) > 0.50 (Barbieri & Berger, 2004; Kalies et al., 2012). These covariates were subsequently used for the second phase. The goodness-of-fit (MacKenzie & Bailey, 2004) of the full model (global model) was assessed to evaluate 1) the plausibility of the model being correct ($p > 0.05$); and 2) on how adequately the model described the observed data, determined by an over dispersion statistic ($\hat{c}$).

In the second phase, the R package “stocc” version 1.23 (Johnson, 2015) was used in R 3.1.2 (R Core Team, 2014) to evaluate the need to account for spatial autocorrelation. The posterior predictive loss criterion (Johnson et al., 2013) was used for model selection between the model without spatial autocorrelation parameter (best model from the previous phase) and the model with spatial autocorrelation parameter. Both models (the model with and without autocorrelation parameter) were fitted using a *probit* link instead of a traditional logit model (Johnson, 2015). The *probit* formulation increases computational efficiency and flexibility through a data augmentation approach, which is not applicable with the *logit* link (Dorazio & Rodríguez, 2012; Johnson et al., 2013).

The spatial autocorrelation parameter was specified using the restricted spatial regression model (RSR), threshold of 3.3 km and moran.cut of 89.2 (0.1 ∗ number camera-trap stations, as recommended by Hughes & Haran, 2013). In the RSR model spatial random effects are constrained to be orthogonal to the fixed effects. Besides providing computational benefit, the RSR usually alleviates spatial confounding and results in more precise estimates of regression coefficient (Hughes & Haran, 2013; Hanks et al., 2015; Paddock et al., 2015). The threshold component (3.3 km) means that all sites within a specified distance threshold of site i are considered neighbors of site i, and was set to represent the average clouded leopard home range (30–40 km^2, which corresponds to 3.1–3.5 km radius. Sanderson et al., 2008). The moran.cut component is the cut-off for selecting the spatial harmonics used in the RSR model (Johnson, 2015). For each Bayesian model, the Gibbs sampler was run for 50,000 iterations following a burn-in of 10,000 iterations that were discarded, and a thinning rate of 5.

The third phase constitutes using important variables in a predictive mapping of suitable habitat for the clouded leopard. First, for each pixel considered to be forest in Peninsular Malaysia (based on 75% GFC threshold), we extracted values of the important covariates using a 90 m resolution. This 75% GFC threshold was chosen because analysis from the first phrase revealed the GFC values at 75% threshold was important in influencing clouded leopard habitat use. Second, to account for spatial autocorrelation, we used the second phase estimates of these covariates and the best model from the second phase to predict clouded leopard occurrence in the forested pixels. Third, we imported these pixels into QGIS (QGIS Development Team, 2014) to assess clouded leopard habitat suitability across the Peninsular Malaysia landscape, in particular at the proposed linkages. We calculated predicted habitat use probabilities for areas within and outside of the CFS as well as for 37 proposed linkages. The CFS consists of two sections, CFS1 covers the northern part of Peninsular Malaysia within the states of Terengganu, Perak, Kedah, Kelantan and northern Pahang and CFS2 covers the southern part within the states of Johor, Negeri Sembilan,

Table 3
Clouded leopard single covariate occupancy (ψ) models. AIC_c akaike's information criterion corrected for finite sample sizes. ΔAIC_c relative difference in AIC_c values compared with the top ranked model, AIC_cwt weight, K number of parameters. Site covariates tested were: elevation (ELEVATION), distance to drainage (DRAINAGE), distance to artificial lakes edge (LAKE), distance to roads (ROAD), distance to village (VILLAGE), Vegetation Continuous Field (VCF), Global Vegetation Change with four different threshold values (GFC30, GFC50, GFC75, GFC90), Disjunct Core Area Density (DCAD), Contrast-weighted edge density (CWED), Contiguity index (CONTIG).

a

	AICc	ΔAICc	AICcWt	K	−2 log likelihood
ψ (DCAD + DRAINAGE + GFC75)	2368.73	0	0.28	13	−1171.16
ψ (DCAD + DRAINAGE + ELEVATION + GFC75)	2368.81	0.07	0.27	14	−1170.16
ψ (DCAD + DRAINAGE + GFC75 + CONTIG)	2370.52	1.79	0.12	14	−1171.02
ψ (DCAD + DRAINAGE + ROAD + GFC75)	2370.56	1.83	0.11	14	−1171.04
ψ (DCAD + DRAINAGE + ELEVATION + GFC75 + CONTIG)	2370.62	1.88	0.11	15	−1170.04
ψ (DCAD + DRAINAGE + GFC75 + VCF)	2370.71	1.97	0.11	14	−1171.11

b

Covariate	Summed model weights
DRAINAGE	0.99
DCAD	0.86
GFC75	0.76
ELEVATION	0.55
CONTIG	0.29
ROAD	0.29
VCF	0.28
LAKE	0.27

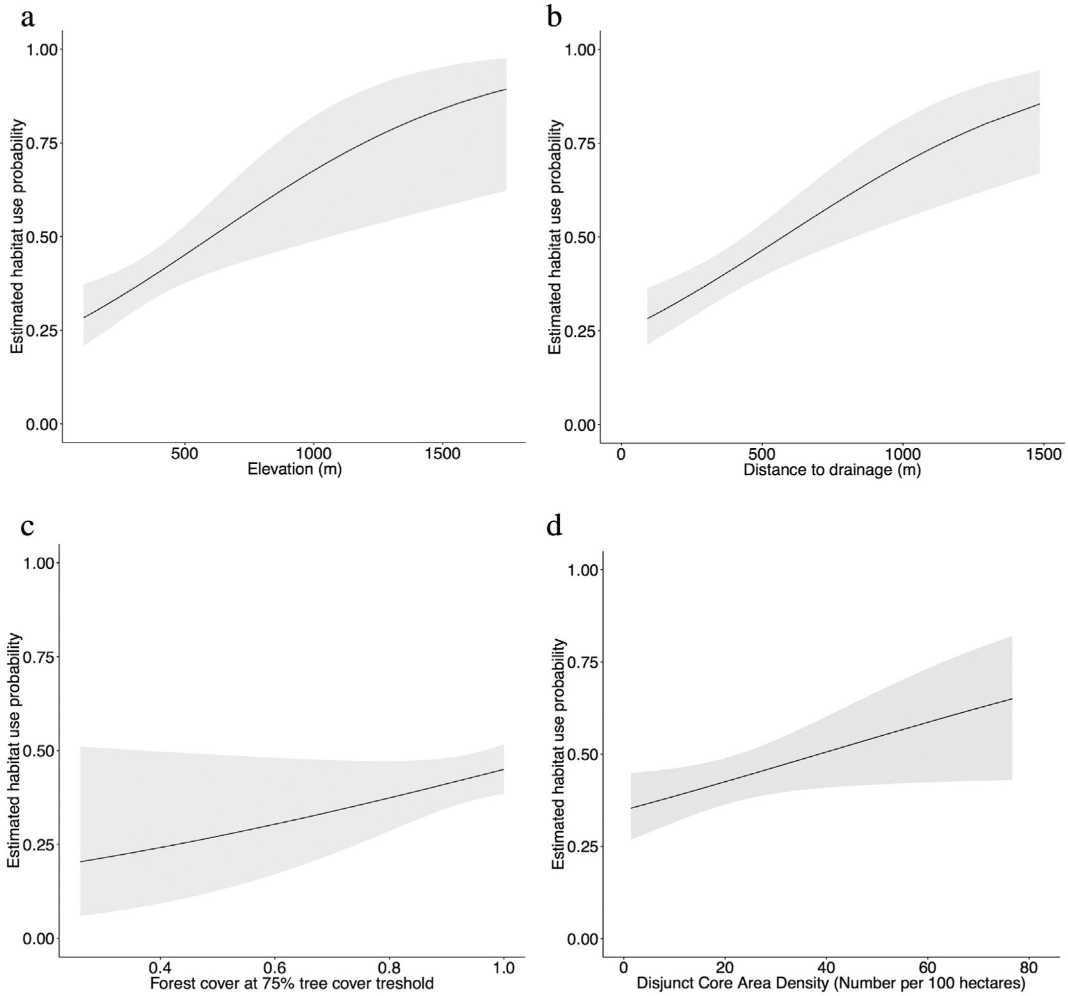

Fig. 2. Relationship between clouded leopard estimated habitat use probability and site covariates with summed model weights >0.5. a) Elevation; b) distance to drainage (DRAINAGE); c) Global Forest Change Threshold 75% (GFC75); d) Disjunct Core Area Density (DCAD).

Selangor and southern Pahang. Primary linkages are areas where it is crucial to re-establish forest connectivity between important forest blocks in order to achieve the main CFS masterplan. Secondary linkages complement primary linkages and are areas where it is unfeasible to establish a primary linkage, but nevertheless important to maintain some level of connectivity, to cater for movement of small animals, birds and insects (DTCP, 2009). We compared the mean habitat use probabilities for the linkages with that of overall average using the confidence interval. In addition, as we were interested in assessing the landscape suitability for clouded leopards, we identified any isolated forested patches that met the following criteria: (1) within 13.6 km of the CFS periphery based on the farthest mean maximum distance moved from other studies (13.6 km; Borah et al. 2014), (2) with predicted habitat use probability above the overall average of 49.3% and confidence interval not overlapping this average and (3) of a minimum size of 50 km^2, based on an average home range of 30–40 km^2 (Grassman et al., 2005; Austin et al., 2007) and considering two individuals as a minimum viable population and a home range overlap of 39% (Grassman et al., 2005).

2.3. Map construction

Time-series land use change maps were constructed for 2000 and 2014. These maps showcase the full state of the peninsula as classified by forest, non-forest, forest loss, forest gain and water (GFC, Hansen et al., 2013). Forest change statistics from 2000 to 2014 were then calculated for the whole peninsula and for the CFS region. From the 2014 map, predicted habitat use probabilities of the clouded leopard was also calculated for areas outside and within the CFS.

3. Results

After restricting camera trap days to 120-day period, collapsing occasions and excluding five stations with extremely high detection rates, 894 camera-trap stations and 351 clouded leopard independent records were included in the analysis, totaling an effort of 69,918 camera trap days. Clouded leopards were recorded at 233 camera-trap stations (overall naïve habitat use probability of 0.26).

A closer inspection on the Goodness of Fit chi-square table revealed that five sites (out of 897) were responsible for 88% of the total test statistics value (Table S2). Four of these sites had 5 detections of clouded leopard on 8 occasions, which corresponded to a detection probability ($p = 0.63$) much higher than the overall detection probability ($p = 0.07$). One of these sites had 3 detections on 5 occasions ($p = 0.60$) Altogether, those five sites inflated chi-squared value and decreased goodness of fit (see Table S2). As suggested by Meredith (2008), the five sites were removed before rerunning the first phase.

There was correlation between all GFC forest cover covariates, between GFC90 and CWED, between LAKE and VILLAGE, between VILLAGE and ROAD as well as between DCAD and CWED (Table S3). Therefore, we chose one covariate among the correlates, based on their performance in the univariate habitat use models, i.e. lower AIC (Table S4).

3.1. Selection of covariates

Both EFFORT and SITE significantly contributed to the variation in the detection probability of clouded leopard (Table 2). Detection was positively affected by effort (beta = 0.20, SE = 0.04) and not constant between surveyed areas: Pasoh and Primary Linkage 7 eastern had the lowest and highest detection probabilities, respectively (Table S5). Table 3a shows the top ranking models for habitat use. Among all site covariates, only ELEVATION, DRAINAGE, GFC75 and DCAD attained summed model weights > 0.5 (Table 3b). Subsequently, these covariates were used in models to test for spatial autocorrelation. There was a positive correlation between habitat use and elevation (Fig. 2a) as well as between habitat use and distance from drainage (DRAINAGE; Fig. 2b). Further, habitat use was positively associated with Global Forest Change 75% threshold values (GFC75; Fig. 2c) and with the density of disjunct core areas (DCAD; Fig. 2d).

3.2. Best model accounting for spatial autocorrelation

The posterior distribution of spatial variance parameter σ was sufficiently far from zero (95% credible interval of 1.71–49,772) to suggest that the spatial process was significantly contributing to the overall variability of the habitat use probabilities across the study sites (Johnson et al., 2013). Based on 95% credible interval, there was strong evidence to suggest that DRAINAGE, GFC75 and DCAD were positively associated with habitat use (Table S6).

Sites located in the northern central part of Peninsular Malaysia exhibited mid-levels of estimated habitat use probabilities (Belum, Temengor, Taman Negara, Primary Linkage 7 western), sites at the east and west periphery of the peninsula (Primary Linkage 7 eastern and Linkage 8 respectively) had high estimated habitat use probabilities whilst sites furthest north and south (Ulu Muda and Pasoh respectively) had low estimated habitat use probabilities (Table S6). For Primary Linkage 7 eastern and western (2nd) surveys, the naïve habitat use probability was similar and slightly lower than the estimated habitat use probability (Fig. S1). For all other sites, the naïve habitat use probability was lower (outside the interquartile range) than the estimated habitat use probability, suggesting imperfect detection (Fig. S1).

3.3. Predicted occurrence across Peninsular Malaysia

Results demonstrated that forest cover decreased by 11,194 km^2 from 63,085 km^2 in 2000 to 51,891 km^2 in 2014 (17.7% loss; Fig. 3a), 2794 km^2 of which occurred within the CFS boundary. By 2014, only 39.7% of 130,598 km^2 Peninsular Malaysia was occupied by forest. Predicted habitat use probability is reflective of the habitat's suitability for the clouded leopard. As a general overview, the western mountainous range (Fig. 3b) running from the Belum-Temengor forest complex in the North to a region west of Pasoh Forest in the South exhibited slightly higher predicted intensity of habitat use than surrounding areas. Another area predicted to have high occurrences of clouded leopard is located at the northeast, encompassing both west and east regions of Primary Linkage 7 (Fig. 3b).

The overall mean predicted habitat use probability in forested areas is 0.493 ± 0.094 SD. Predicted habitat use probability within the Central Forest Spine (CFS) was 0.506 ± 0.094 SD versus 0.456 ± 0.087 SD

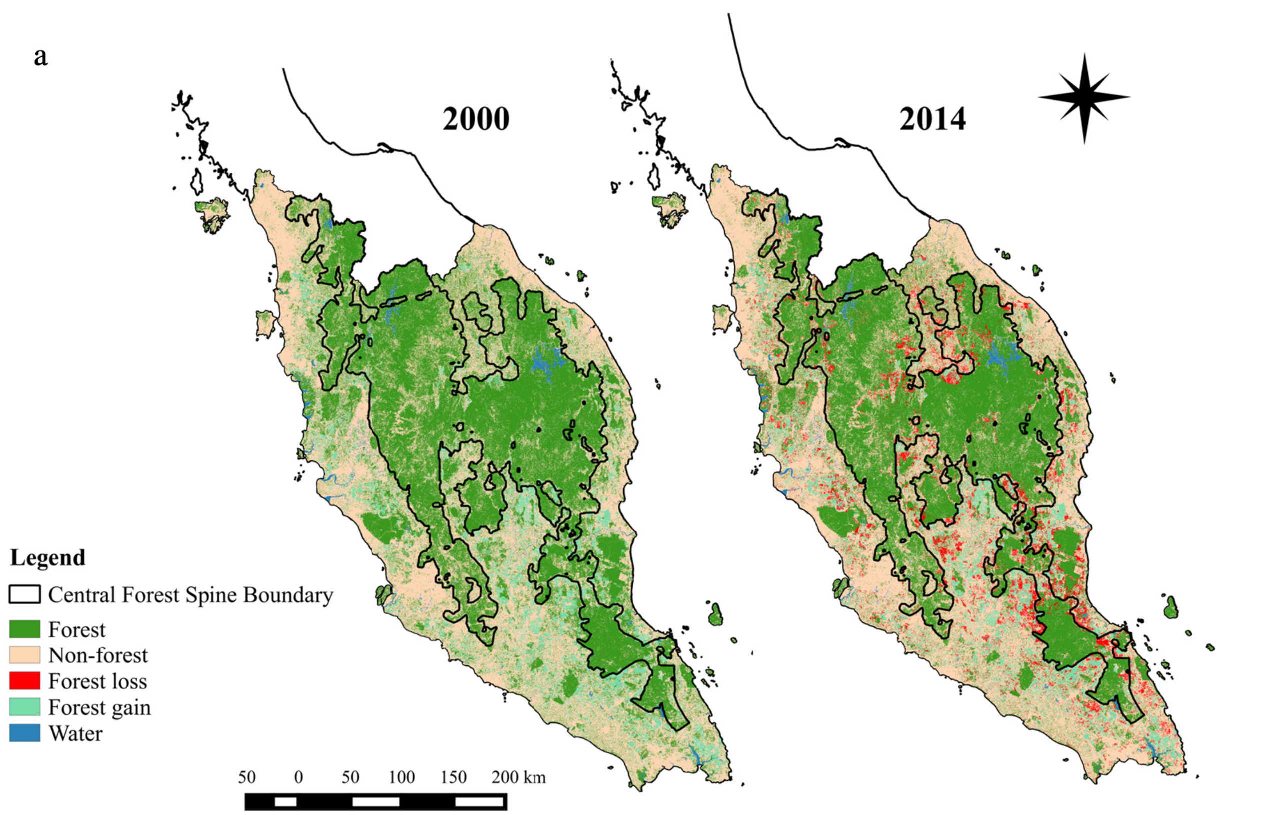

Fig. 3. Forest coverage and predicted clouded leopard habitat use in Peninsular Malaysia. a) Forest cover in 2000 and 2014; b) Predicted clouded leopard habitat use probabilities and forest linkages. CFS: Central Forest Spine (1 is in the north and 2 is in the south separated by the horizontal line across Peninsular Malaysia.); PL: Primary Linkage; SL: Secondary Linkage. Four forest patches with high predicted habitat use probabilities are marked: 1 – Hutan Lipur Ulu Nanas; 2 – Hutan Lipur Papan; 3 – Hutan Lipur Sungai Satu; 4 – Pasoh Forest Reserve; c) Four forest patches shown in details. Top left figure shows Hutan Lipur Ulu Nanas (left) and Hutan Lipur Papan (right); top right figure shows Hutan Lipur Sungai Satu; bottom left figure shows Pasoh Forest Reserve.

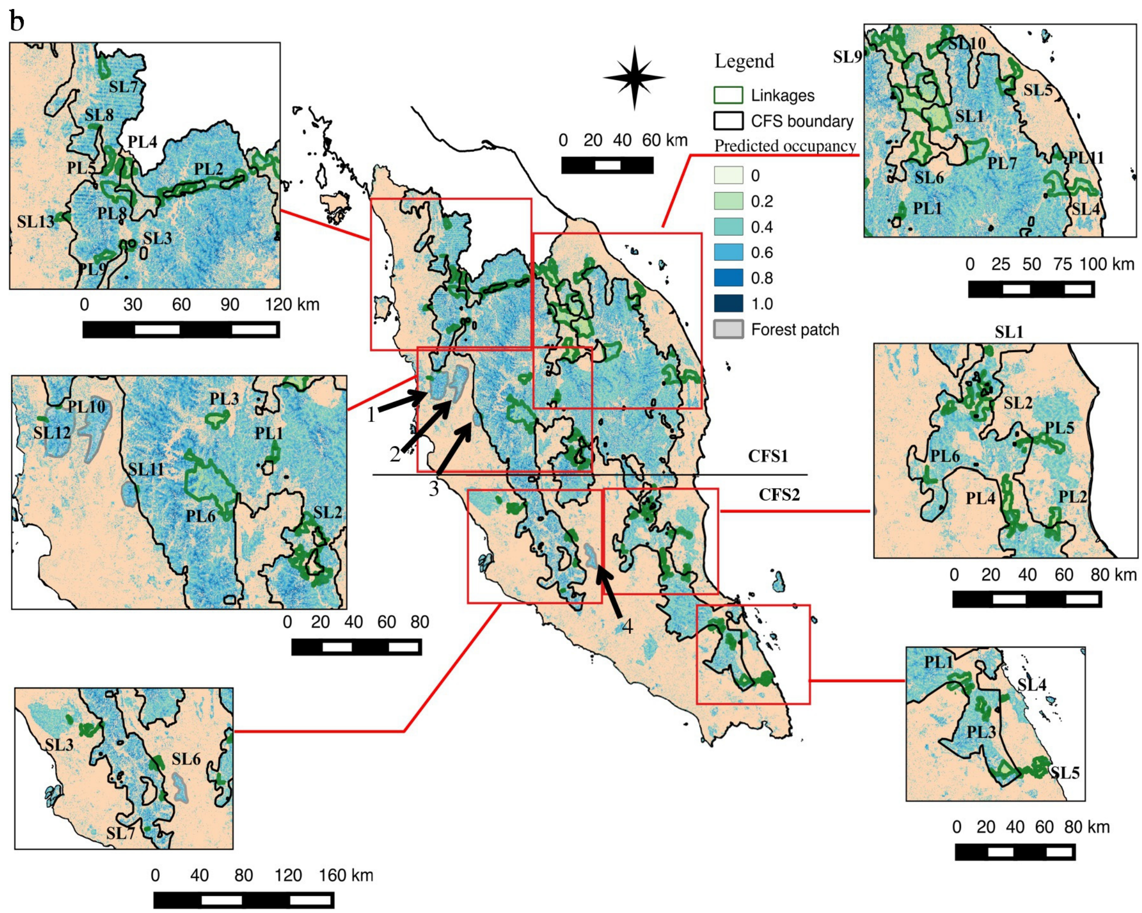

Fig. 3 (*continued*).

outside the CFS boundary. The 37 linkages connected areas of reasonable suitability for clouded leopard use (Fig. 3b). However, most of the linkages were lacking in forests (26 of the linkages were <50% covered by forest) and attained less than average predicted habitat use probability (23 linkages had confidence interval lower than and not overlapping the overall average; Table 4). We identified four sites just outside the periphery of CFS that were relatively high in predicted intensity of habitat use (Fig. 3b), Hutan Lipur Ulu Nanas (0.549 ± 0.091 SD; area: 449.2 km^2), Hutan Lipur Papan (0.533 ± 0.091 SD; area: 362.1 km^2), Hutan Lipur Sungai Satu (0.546 ± 0.090 SD; area: 98.3 km^2) and Pasoh Forest (0.526 ± 0.091 SD; area: 171.7 km^2). Of the four forests, Hutan Lipur Ulu Nanas and Hutan Lipur Sungai Satu are connected via a linkage to the CFS (Fig. 3c).

4. Discussion

This study combined camera-trap data from nine different surveys in Peninsular Malaysia to assess populations of the elusive clouded leopard on a regional scale. Our results revealed four important covariates that positively influence clouded leopard habitat use as well as demonstrate the need to control for spatial autocorrelation. We also showed that the area proposed under the CFS has the potential to offer good protection for the clouded leopard in Peninsular Malaysia. However, linkages had below-average levels of forested area and habitat suitability for the clouded leopard.

The results indicated that detection probability is positively correlated by camera trapping effort and it was not constant across all survey areas. This influence is expected because full sampling occasions (15-day periods) have a higher probability of detecting a species than incomplete sampling occasions. Therefore, it is important to account for this source of variance in the dataset. The different detection probabilities across sites might be a result of other factors such as clouded leopard behavior (e.g. clouded leopard response to different levels of disturbance at various sites) or seasonality (e.g. period of the year that the surveys were carried out: e.g. monsoon season or not). The local density of the species at each site will also influence detectability, i.e., higher numbers of clouded leopards in a particular area would lead to higher detection probabilities (Bailey et al., 2004). Additionally, other species might have a strong influence on its presence, for example prey availability was positively associated with clouded leopard habitat use in the study of Mohamad et al. (2015). Sites also differed in terms of whether tigers or leopards were present (e.g. Tan et al., 2015), which might in turn affect the activity of the clouded leopards. Whilst the focus of this study was on the influence of geographical features, further studies could take into account interspecies interactions to understand the biological factors affecting detection of clouded leopard.

Elevation was an important covariate for clouded leopard habitat use. Positive association of clouded leopard habitat use and elevation has also been previously reported in West-Central Sumatra (Haidir et al., 2013). Hutajulu et al. (2007) suggested that clouded leopards use higher elevations to avoid the tiger (but see Sunarto et al., 2012). Alternatively, Mohamad et al. (2015) argued that elevation is a distal factor that likely influences prey availability, and in turn clouded leopard occurrence. This is one caveat of our study: we did not obtain direct measures of prey availability. Another possible reason for the relation between elevation and clouded leopard habitat use is that elevation is generally correlated to the gradient of slopes, which is negatively correlated to human activities (Sunarto et al., 2012). As a consequence, flat low-elevation forested areas are likely to suffer higher level of human-caused disturbance than steep high-elevation forests (Holmes, 2002), the latter might favor the presence of clouded leopards. Similar logic could be used to explain the positive relationship between clouded

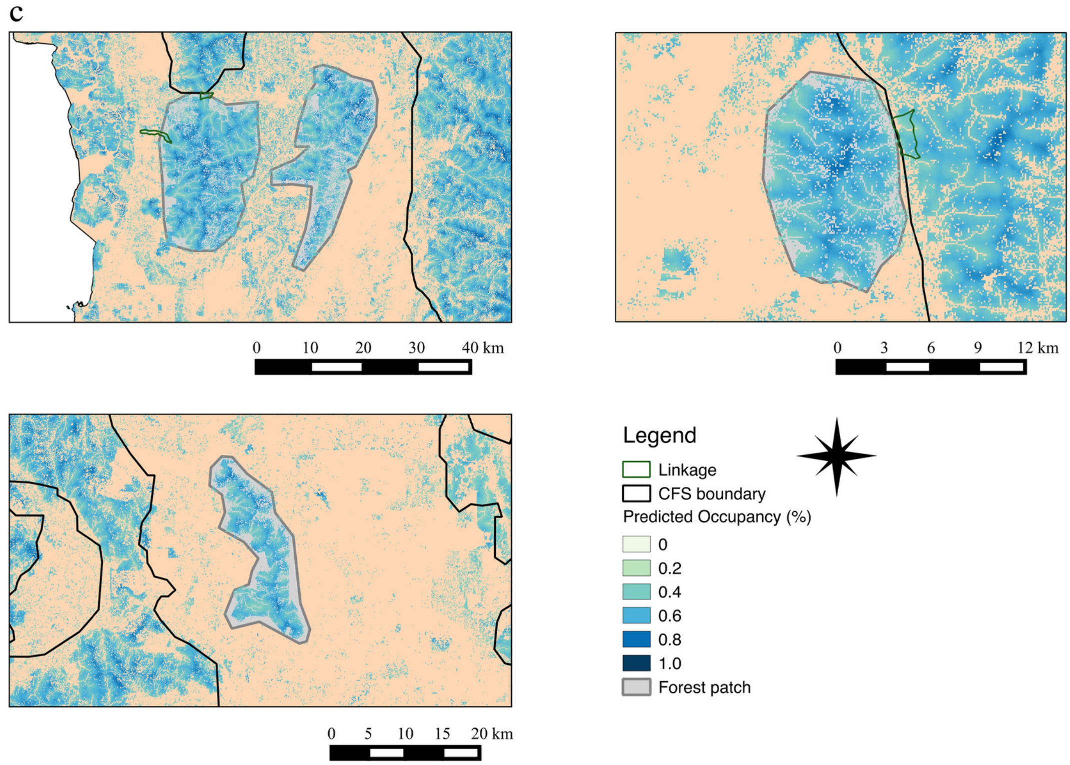

Fig. 3 (*continued*).

leopard habitat use and distance to drainages, another important site covariate affecting clouded leopard occurrence in our study. It has been proposed that human activities are concentrated around water bodies, making such areas less conducive for large predators (Sunarto et al., 2012). However, these might not be the case for smaller streams and rivers deep within many of our forest sites and largely inaccessible to people. Hence, the reason for this relationship between drainage and habitat use remains unclear.

Previous studies have found that clouded leopards used forests more than other types of vegetation such as grassland and secondary forest (Austin et al., 2007), avoid forest edges (Haidir et al., 2013) and were found less frequently in less intact forest covers (Clements, 2013). However, clouded leopards in Malaysia can be resilient to some levels of degradation, such as logged forests (Mohamad et al., 2015). Our results further shed light on this issue: we found a positive relationship between Global Forest Change at 75% threshold (GFC75) and habitat use suggesting that a higher percentage of forested area in the 500 m buffer of each camera site is more suitable for clouded leopard use. There was also a positive correlation between disjunct core areas density (DCAD) and habitat use indicating that a higher density of subdivided patches of core area would be ideal for the species. Both findings confirm the idea that clouded leopards prefer interior forested habitats in high densities. Additionally, we found no effects of continuity (CONTIG) and edge density (CWED) on habitat use, the latter confirming that forest edges do not deter the clouded leopard.

There is a caveat in applying occupancy models to camera trap survey data: our inference is based on records from a point location (single camera trap station) and covariates are obtained within a larger spatial scale (within and area of 0.5 km radius around each trap). The models assume that the conditions across the 0.78 km^2 around the point location are similar and hence have the same probability of species' detection. The use of multiple cameras or collection of other clouded leopard signs within the area of inference could potentially provide a more accurate occupancy estimate. We also stress that results are based on the specific spatial scale used in this study (area of 0.5 km radius around camera trap station). Therefore, the relationship between influential covariates and clouded leopard estimated habitat use may not hold true for other spatial scales.

This study has compiled multiple camera-trapping surveys to create the largest dataset ever published for the clouded leopard. Besides shedding light on the understudied spatial distribution of clouded leopards, our regional scale approach gives a broader understanding of the habitat use of the species, which is especially pertinent to the management of endangered species across a landscape scale. Moreover, the large amount of data allowed for a powerful analysis and was less prone to spurious effects (significant because of randomness and hence false positives) or site-specific effects (for e.g. the distance to roads). The results of this study were used to predict the intensity of clouded leopard habitat use at sites that have not been surveyed, based on their covariates values. However, this regional scale approach does not replace site-specific studies (e.g. Mohamad et al., 2015). Whenever possible, management decisions at site-specific level should be made based on local studies that take into account local peculiarities and specific threats for the species.

The CFS presents a blueprint for where protection of forests should be focused and it encompasses favorable habitats suitable for the clouded leopard. The average predicted habitat use probability within the boundary is 11.0% higher than forested sites outside of the boundary. Forest loss within this CFS needs to be minimized or halted; 2794 km^2 of the forest areas within the CFS has been lost from 2000 to 2014. Further efforts could also be made to reforest and enhance the habitat suitability of proposed linkages, which currently exhibit poor suitability for the clouded leopard. Importantly, a higher percentage of forested areas within linkages would both increase percentage forest cover and enhance the density of core areas, both key to the occurrence of the clouded leopard. Notably, because of our usage of 2-dimensional maps, this study could not account for forest cover underneath human infrastructure such as highway viaducts (Clements et al., 2012). Therefore, our calculation of the percentage forested area of this linkage could be an underestimate and further works could be undertaken to assess viaducts that are obscured by human infrastructure.

Insofar as improving the habitat range of the clouded leopard is a priority, we have identified Hutan Lipur Ulu Nanas and Hutan Lipur

Table 4
Predicted habitat use mean of 37 linkages. Bold numbers indicate that the 95% confidence interval of the mean predicted habitat use probability was below and not overlapping the overall average of 0.493. Underlined values indicate that the confidence interval mean predicted habitat use probability was higher and not overlapping the overall average of 0.493 CFS: Central Forest Spine (1 is in the north and 2 is in the south). PL – Primary linkage; SL – Secondary linkage.

Linkage	Area of linkage (ha)	Area occupied by forest (ha)	Percentage of linkage area that is forested	Mean predicted habitat use probabilities	Predicted habitat use probabilities SD
CFS1-PL1	4399.7	2663.0	60.5	**0.452**	0.069
CFS1-PL2	28269.6	13691.8	48.4	0.538	0.096
CFS1-PL3	6873.3	1432.7	20.8	0.502	0.070
CFS1-PL4	7703.3	2866.4	37.2	0.503	0.074
CFS1-PL5	4698.0	3236.1	68.9	0.502	0.092
CFS1-PL6	53496.0	33646.4	62.9	0.523	0.093
CFS1-PL7	22795.9	14685.2	64.4	**0.447**	0.076
CFS1-PL8	15515.7	7223.8	46.6	0.529	0.080
CFS1-PL9	3698.3	2168.9	58.6	0.521	0.101
CFS1-PL10	202.9	85.8	42.3	**0.455**	0.062
CFS1-PL11	1250.5	614.3	49.1	**0.490**	0.084
CFS1-SL1	104671.9	26413.2	25.2	**0.488**	0.091
CFS1-SL2	19095.5	7260.7	38.0	0.517	0.088
CFS1-SL3	3688.7	1307.5	35.4	0.526	0.090
CFS1-SL4	32442.4	17843.3	55.0	**0.444**	0.070
CFS1-SL5	18391.6	5909.4	32.1	**0.453**	0.081
CFS1-SL6	20720.1	2839.8	13.7	0.506	0.085
CFS1-SL7	4455.0	3043.1	68.3	**0.471**	0.091
CFS1-SL8	1140.3	481.3	42.2	**0.453**	0.060
CFS1-SL9	31366.7	11129.1	35.5	**0.492**	0.088
CFS1-SL10	16592.1	9626.9	58.0	0.498	0.075
CFS1-SL11	298.4	241.1	80.8	**0.445**	0.055
CFS1-SL12	388.3	159.6	41.1	**0.449**	0.050
CFS1-SL13	1627.2	417.8	25.7	**0.476**	0.093
CFS2-PL1	14351.8	3686.5	25.7	0.430	0.055
CFS2-PL2	6687.0	1932.9	28.9	**0.454**	0.079
CFS2-PL3	6736.9	1890.9	28.1	0.498	0.097
CFS2-PL4	10402.3	1023.5	9.8	**0.452**	0.063
CFS2-PL5	6642.7	1811.1	27.3	**0.457**	0.077
CFS2-PL6	1245.2	652.9	52.4	**0.450**	0.072
CFS2-SL1	1049.7	340.6	32.4	**0.472**	0.055
CFS2-SL2	15045.7	5064.4	33.7	**0.456**	0.079
CFS2-SL3	3594.8	417.8	11.6	**0.452**	0.073
CFS2-SL4	1166.5	127.8	11.0	**0.460**	0.064
CFS2-SL5	8672.4	1015.8	11.7	**0.460**	0.069
CFS2-SL6	4803.6	1074.1	22.4	**0.453**	0.062
CFS2-SL7	322.9	177.6	55.2	**0.488**	0.055

Sungai Satu, which have proposed linkages with the CFS as well as Hutan Lipur Papan and Pasoh forest reserve as forest patches ideal for this species (see results; Fig. 3b, c). In particular, the latter two sites are located very close to but are separated by roads from the CFS and there are no proposed linkages to these areas. It is important to acknowledge that inclusion of these sites into the CFS does not confer protection to them: permanent reserved forests within the CFS are still undergoing logging and being converted to monocultures (see results; Aziz et al., 2010). Protection of these areas can only be achieved by state level commitment, legislation and management. For example, the Belum Forest Reserve within the Belum-Temengor complex is an area that received formal protection from state of Perak, only after intensive lobbying by conservation advocates (Bernama, 2007). Identifying important sites is only the first step towards attaining protection.

Our case study on the habitat use of the clouded leopard in Peninsular Malaysia provides important insights for the management of this Vulnerable species. Using the largest dataset consolidated for this species and recently developed habitat use modelling that accounts for spatial autocorrelation, we have identified suitable habitats and assessed the current suitability of proposed linkages for the species across the country. This presents valuable information for land use planning and management, enabling us to determine the suitability of forest remnants and linkages to support populations of clouded leopard and contributes towards the understanding of how this species responds to increasing threats such as human development and changing landscapes. Effective protection of the CFS areas could begin with states implementing the project and stopping the ongoing degradation, especially in the ecological linkages. Findings of this study will be provided to the relevant stakeholders so as to facilitate this process.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.12.012.

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