BIODIVERSITY RESEARCH

Diversity and Distributions **WILEY**

Multi-scale habitat modelling identifies spatial conservation priorities for mainland clouded leopards (*Neofelis nebulosa*)

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Abstract

Aim: Deforestation is rapidly altering Southeast Asian landscapes, resulting in some of the highest rates of habitat loss worldwide. Among the many species facing declines in this region, clouded leopards rank notably for their ambassadorial potential

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and capacity to act as powerful levers for broader forest conservation programmes. Thus, identifying core habitat and conservation opportunities are critical for curbing further *Neofelis* declines and extending umbrella protection for diverse forest biota similarly threatened by widespread habitat loss. Furthermore, a recent comprehensive habitat assessment of Sunda clouded leopards (*N. diardi*) highlights the lack of such information for the mainland species (*N. nebulosa*) and facilitates a comparative assessment.

Location: Southeast Asia.

Methods: Species–habitat relationships are scale-dependent, yet <5% of all recent habitat modelling papers apply robust approaches to optimize multivariate scale relationships. Using one of the largest camera trap datasets ever collected, we developed scale-optimized species distribution models for two con-generic carnivores, and quantitatively compared their habitat niches.

Results: We identified core habitat, connectivity corridors, and ranked remaining habitat patches for conservation prioritization. Closed-canopy forest was the strongest predictor, with ~25% lower *Neofelis* detections when forest cover declined from 100 to 65%. A strong, positive association with increasing precipitation suggests ongoing climate change as a growing threat along drier edges of the species' range. While deforestation and land use conversion were deleterious for both species, *N. nebulosa* was uniquely associated with shrublands and grasslands. We identified 800 km^2 as a minimum patch size for supporting clouded leopard conservation.

Main conclusions: We illustrate the utility of multi-scale modelling for identifying key habitat requirements, optimal scales of use and critical targets for guiding conservation prioritization. Curbing deforestation and development within remaining core habitat and dispersal corridors, particularly in Myanmar, Laos and Malaysia, is critical for supporting evolutionary potential of clouded leopards and conservation of associated forest biodiversity.

KEYWORDS
clouded leopard, conservation planning, deforestation, multi-scale modelling, *Neofelis diardi*, *Neofelis nebulosa*, spatial conservation prioritization, threatened and endangered species

1 | INTRODUCTION

Deforestation, fire, and land conversion (e.g., to large-scale oil palm and *Acacia* monocultures) are rapidly altering South and Southeast Asian landscapes (Cushman, Macdonald, Landguth, Malhi, & Macdonald, 2017; Tacconi, 2003), resulting in some of the highest rates of habitat loss worldwide (Gaveau et al., 2016; Miettinen, Shi, & Liew, 2011). Among the many species facing declines in this region, clouded leopards rank notably for their charisma (Macdonald et al., 2015), umbrella capacity (Dickman, Hinks, Macdonald, Burnham, & Macdonald, 2015), and ambassadorial potential (Macdonald et al., 2017). Species of conservation concern in their own right, clouded leopards are also powerful levers of conservation action for broader forest conservation programmes, including umbrella protection for diverse forest biota similarly threatened by widespread habitat loss (Collins, Milner-Gulland, Macdonald, & Macdonald, 2011).

The mainland clouded leopard, *Neofelis nebulosa*, ranges from the Nepali Himalayas in the west to southern China in the north and east, and extends south into Peninsular Malaysia; its sister species, the Sunda clouded leopard (*N. diardi*), occurs on Borneo and Sumatra (Buckley-Beason et al., 2006; Can et al., ; Kitchener, Beaumont, & Richardson, 2006). Both species are listed as Vulnerable on the IUCN Red List of Threatened Species (Grassman et al., 2016; Hearn et al., 2015), and India recently added *N. nebulosa* to its Recovery Programme for Critically Endangered Species (National Board for Wildlife, 2018). It is estimated that fewer than 10,000 adults remain of either *N. nebulosa* (Grassman et al., 2016) or *N. diardi* (Hearn et al., 2015). The two species diverged ~1.9 mya (Wilting et al., 2011), and while the degree of differentiation between the two species suggests they are as genetically distinct as lions and tigers (Buckley-Beason et al., 2006), similarities and differences between their

ecological niches remain largely unknown. Understanding the habitat preferences of these reclusive and vulnerable felids is critical to inform conservation planning to mitigate further losses.

There have been several local abundance estimates of *N. nebulosa* based on camera trapping. Estimated population densities for India (Singh & Macdonald, 2017), Myanmar (Naing, Ross, Burnham, Htun, & Macdonald, 2017), Bhutan (Penjor, Macdonald, Wangchuk, Tandin, & Tan, 2018) and Nepal (Can et al.,) range between 0.30 and 5.14 individuals/100 km^2, and indicate general associations with forest habitats. These build on previous estimates of 4.73/100 km^2 in India (Borah et al., 2014) and 2.64 (L. Hedges, unpublished data) to 3.46/100 km^2 in Malaysia (Mohamad et al., 2015). Yet, a comprehensive, range-wide assessment of habitat selection is lacking.

A recent assessment of habitat associations for *N. diardi* revealed that both recent forest loss and large-scale plantations strongly and negatively influenced detection rates (Macdonald, Bothwell, et al., 2018). Conversely, *N. diardi* were positively associated with forests, higher elevations and ridgelines. That study also found significant differences in poaching among regions, with substantially greater poaching pressure in Sumatra compared to Borneo; *N. diardi* detections decreased rapidly when even a few poachers were observed (Macdonald, Bothwell, et al., 2018). The recent comprehensive assessment of habitat use for the Sunda species now makes possible the comparison with *N. nebulosa* presented here.

To compare ecological niches between the two clouded leopard species, we developed a multi-scale habitat selection model that encompasses the full range of *N. nebulosa* from Nepal to Malaysia, following the same approach previously applied to *N. diardi* on Borneo and Sumatra (Macdonald, Bothwell, et al., 2018). It has long been recognized that species–habitat relationships are scale-dependent (Levin, 1992; Wiens, 1976, 1989), and scale optimization has been shown to substantially increase model predictive power when compared with non-optimized, single-scale models (Timm, McGarigal, Cushman, & Ganey, 2016; Wan et al., 2017). Yet, a recent review found that <5% of current habitat modelling papers used robust approaches to optimize multivariate scale relationships (McGarigal, Wan, Zeller, Timm, & Cushman, 2016). Scalar relationships are a critical component of habitat use and provide valuable information for conservation management planning and reserve design; therefore, it is critical to incorporate multi-scale approaches into the statistical modelling framework when describing species–environment relationships (Thompson & McGarigal, 2002). Using *N. nebulosa* as an example, we demonstrate a two-step, multi-scale modelling framework, recommended as the most robust method currently available for multi-scale optimization (McGarigal et al., 2016). We first utilize a univariate approach to identify the optimal spatial scale for each environmental predictor, and second, combine scale-optimized predictor variables in a multivariate model to describe *N. nebulosa's* association with its environment.

Here, we aimed to identify *N. nebulosa's* primary habitat requirements, limiting factors and sources of threat. Specifically, we sought to (a) identify key environmental and anthropogenic variables influencing *N. nebulosa* habitat use, (b) determine the spatial

scale at which each variable most strongly influences clouded leopard detection, and (c) draw comparisons between *N. nebulosa* and findings previously reported for *N. diardi*. The comparison between their habitat associations, which we make here for the first time, offers valuable insights into the ecology of these elusive species. Furthermore, these results provide critical information to assist in conservation management of *N. nebulosa* and the associated forest biodiversity for which it is an ambassador (Macdonald et al., 2017).

2 | METHODS

2.1 | Data collection

From 2008 to 2016, we deployed 2,948 camera stations across 45 sampling locations in nine countries spanning *N. nebulosa's* full range throughout South and Southeast Asia (Table 1). Ten original sampling locations were surveyed by the Wildlife Conservation Research Unit (WildCRU, University of Oxford), 21 sites were contributed by collaborators in Bhutan (Penjor et al., 2018), nine sites in Peninsular Malaysia were contributed by Tan et al. (2017), and E. Ash (unpublished data) contributed surveys from five locations in Thailand. Camera stations were primarily located in national parks, reserves, and other protected areas. In Bhutan, camera traps were widely deployed, irrespective of land protection status, resulting in 10/21 sampling locations in protected areas (Penjor et al., 2018). Given the challenge of detecting clouded leopards in dense forests (Wilting et al., 2011), cameras were primarily deployed along ridgelines, streams, and forest breaks (e.g., man-made trails, abandoned logging roads), where detection rates have been shown to be higher (Hearn, Cushman, Ross et al., 2018; Macdonald, Bothwell, et al., 2018). Imperfect detection can bias estimates of true occupancy probability; however, our aim was rather to assess the overall strength and direction of relationships with environmental factors to provide guidance for *N. nebulosa* habitat conservation. For the purpose of assessing species–habitat relationships in rare or difficult-to-detect species, Banks-Leite et al. (2014) found that accounting for imperfect detection (e.g., with occupancy modelling) did not provide significantly more accurate results. Furthermore, unadjusted capture frequencies tend to be highly correlated with adjusted estimates (Kelly, 2008). Thus, while we acknowledge the potential for variance in probability of detection among camera stations, relative strength and direction of relationships should be preserved. Paired camera stations were situated ~40 cm above ground and spaced 1-2 km apart. This camera density was originally designed for estimating spatial capture–recapture density. Data were spatially rarefied to one station/1.0 km^2 to negate pseudo-replication for subsequent modelling, resulting in removal of 56 camera stations. We further tested for and found very low levels of spatial autocorrelation (Moran's $\bar{I}$ = 0.02; Table 1; 'spdep' R package; Bivand & Piras, 2015), thereby validating the assumption of independence among samples.

TABLE 1 Collection information, including nine countries, 45 sampling locations, camera traps/site (*n*), total *N. nebulosa* detections, detection rate, mean number of trap nights (camera effort), and Moran's *I* spatial autocorrelation and significance

Country	Sampling location	*n*	Total de-tections	Detection rate	Mean # trap nights (±*SE*)	Moran's *I*	*p*
Bhutan (*n* = 848)	Samtse Division[a]	8	1	0.13 (1/8)	91.88 ± 7.99	NA	NA
	Jigme Khesar Strict Nature Reserve (JKSNR)	19	0	0	74.11 ± 7.36	NA	NA
	Paro Division[a]	48	0	0	58.31 ± 4.47	NA	NA
	Jigme Dorji National Park (JDNP)	32	1	0.03 (1/32)	46.50 ± 4.46	NA	NA
	Thimphu Division[a]	21	0	0	58.05 ± 10.18	NA	NA
	Wangdue Division[a]	77	4	0.04 (3/77)	58.55 ± 4.27	−0.01	0.48
	Gedu Division[a]	33	2	0.06 (2/33)	67.30 ± 5.91	−0.03	0.46
	Tsirang Division[a]	36	8	0.14 (5/36)	86.39 ± 6.33	−0.14	0.69
	Phibsoo Wildlife Sanctuary (PWS)	31	26	0.39 (12/31)	94.52 ± 4.52	0.29	0.08
	Sarpang Division[a]	32	11	0.22 (7/32)	86.65 ± 4.51	−0.02	0.44
	Jigme Singye Wangchuck National Park (JSWNP)	71	47	0.41 (29/71)	81.73 ± 3.23	0.15	0.18
	Royal Manas National Park (RMNP)	56	37	0.30 (17/56)	91.63 ± 3.57	−0.07	0.69
	Wangchuck Centennial National Park (WCNP)	41	1	0.02 (1/41)	33.20 ± 4.02	NA	NA
	Bumthang Division[a]	36	0	0	72.17 ± 6.06	NA	NA
	Zhemgang Division[a]	98	16	0.10 (10/98)	71.34 ± 3.33	−0.06	0.67
	Mongar Division[a]	29	4	0.10 (3/29)	59.07 ± 5.73	−0.13	0.67
	Phrumsengla National Park (PNP)	24	6	0.13 (3/24)	68.92 ± 8.62	−0.17	0.76
	Bumdeling Wildlife Sanctuary (BWS)	28	10	0.18 (5/28)	96.86 ± 6.42	0.09	0.15
	Trashigang Division[a]	26	7	0.23 (6/26)	83.23 ± 5.85	−0.08	0.51
	Sakteng Wildlife Sanctuary (SWS)	22	0	0	58.18 ± 9.08	NA	NA
	Samdrupjongkhar Division[a]	78	12	0.12 (9/78)	74.00 ± 3.66	−0.06	0.58
Cambodia (*n* = 153)	Central Cardamom Protected Forest	76	11	0.13 (10/76)	101.84 ± 0.78	0.01	0.43
	Phnom Prich Wildlife Sanctuary	77	1	0.01 (1/77)	68.61 ± 0.99	NA	NA
India (*n* = 74)	Dampa Tiger Reserve	74	81	0.38 (28/74)	67.05 ± 2.04	0.03	0.33
Laos (*n* = 228)	Nam Phoung-Na Vaen	78	23	0.10 (8/78)	47.81 ± 0.68	−0.06	0.65
	Pha Daeng	78	17	0.19 (15/78)	47.00 ± 0.72	−0.02	0.48
	Phou Pha-Si Phou	72	21	0.22 (16/72)	47.86 ± 0.84	0.07	0.31
Myanmar (*n* = 162)	Htamanthi Wildlife Sanctuary	162	103	0.41 (67/162)	89.79 ± 0.32	0.06	0.30
Nepal (*n* = 83)	Langtang National Park	83	17	0.08 (7/83)	85.60 ± 2.59	−0.03	0.53
Peninsular Malaysia (*n* = 792)	Primary Linkage 7 Corridor	62	46	0.44 (27/62)	174.34 ± 1.78	0.05	0.33
	Primary Linkage 7 Upper Block	81	59	0.40 (32/81)	67.12 ± 1.00	0.08	0.30
	Ulu Muda Forest Reserve Grid 1	78	11	0.13 (10/78)	118.51 ± 4.44	−0.02	0.48
	Ulu Muda Forest Reserve Grid 2	54	28	0.28 (15/54)	111.02 ± 2.04	0.05	0.32
	Royal Belum State Park	165	66	0.21 (34/165)	71.38 ± 4.08	−0.05	0.66
	Temengor Forest Reserve	81	61	0.37 (30/81)	74.77 ± 5.00	−0.01	0.47
	Pasoh Forest Reserve	55	1	0.02 (1/55)	24.25 ± 1.07	NA	NA
	Taman Negara National Park	34	40	0.44 (15/34)	152.06 ± 16.55	0.34	0.01
	Linkage 8	182	70	0.28 (51/182)	61.41 ± 0.40	0.03	0.37
Thailand (*n* = 554)	Khao Yai National Park	67	12	0.15 (10/67)	93.99 ± 13.86	−0.08	0.67
	Dong Yai Wildlife Sanctuary	58	3	0.05 (3/58)	45.66 ± 3.93	0.45	0.0002
	Pang Sida National Park	163	65	0.15 (24/163)	108.90 ± 13.39	−0.02	0.58
	Ta Phraya National Park	56	7	0.09 (5/56)	82.79 ± 8.22	−0.05	0.61
	Thap Lan National Park E	174	36	0.11 (19/174)	97.06 ± 13.81	0.04	0.28
	Thap Lan National Park W	36	1	0.03 (1/36)	39.56 ± 4.19	NA	NA
Vietnam (*n* = 56)	Vietnam	56	0	0	121.80 ± 12.02	NA	NA
Totals		2,948	973		79.47 ± 1.37		

[a]Divisions are management units outside protected areas in Bhutan.

2.2 | Covariates

From previous regional studies, we identified a suite of predictor variables related to *N. nebulosa* habitat use. Closed-canopy forests are a primary requirement for this semi-arboreal species (Cushman et al., 2017; Sollmann, Linkie, Haidir, & Macdonald, 2014; Tan et al., 2017). Conversely, deforestation and subsequent land conversion to large-scale palm and *Acacia* plantations have been identified as major threats for both the mainland (Tacconi, 2003) and Sunda (Cushman et al., 2017; Hearn et al., 2017; Hearn, Cushman, Goossens, et al., 2018; Hearn et al., 2019; Macdonald, Bothwell, et al., 2018; Macdonald, Cushman, et al., 2018) species. Previous studies of *N. nebulosa* in Bhutan (Penjor et al., 2018) and of *N. diardi* in Borneo and Sumatra (Hearn et al., 2016; Hearn, Cushman, Ross et al., 2018; Macdonald, Bothwell, et al., 2018; Macdonald, Cushman, et al., 2018; Sollmann et al., 2014) also found positive associations with ridgelines and slope, and negative associations increased with density of human settlements and land use intensity. Based on careful biological consideration of these relationships, we identified 13 predictor variables that we hypothesized are driving *Neofelis* habitat use. We then transformed these into 46 more biologically informative variables using class- and landscape-level spatial statistics (Table S1). To facilitate comparison with the recently published *N. diardi* habitat model (Macdonald, Bothwell, et al., 2018), we used the same covariates here, plus mean annual precipitation and temperature (MAP and MAT) to account for substantial climatic variability across the large study region.

From a digital elevation model (Jarvis, Reuter, Nelson, & Guevara, 2008), we derived several covariates accounting for topographic heterogeneity (roughness, slope position, compound topographic index (CTI)) using the Geomorphometry and Gradient Metrics Toolbox (Evans, Oakleaf, Cushman, & Theobald, 2014) in ARCGIS 10.2.2 [ESRI, 2011]. CTI characterizes flow accumulation; low elevation drainages incur high CTI, whereas mountaintops and ridgelines exhibit low CTI. Percentage forest cover (Hansen et al., 2013) was reclassified into non-forest (0%–20%), open forest (20%–40%) and closed forest (>40%). For reclassified categorical variables (forest cover, land cover classes, forest loss and protected areas), we used FRAGSTATS (McGarigal, Cushman, Neel, & Ene, 2012) to calculate percentage of the landscape occupied by each variable (PLAND) and correlation length of each class (GYRATE_AM; i.e., average distance an individual could travel within habitat patches or habitat extent). At the landscape level, we calculated contrast-weighted edge density (CWED) among landscape classes to investigate how spatial composition and configuration of the landscape influence *N. nebulosa* detection. CWED measures the impact of habitat edges, weighted by similarity or contrast among habitat types. We generated hypothesized edge density weightings such that moving between very similar habitat types incurred a minimum weighting of 0, whereas maximally contrasting habitats incurred a weighting of 1 (Table S2). For example, we hypothesized that *N. nebulosa* would perceive the difference between closed forest and urban areas as high contrast (CWED = 1), whereas moving from shrubland/grassland to mosaic

cropland would be a less abrupt transition (CWED = 0.5). Because CWED is a metric related to habitat fragmentation, we hypothesized that clouded leopard detection would exhibit a negative association with higher CWED values.

To assess scalar relationships between *N. nebulosa* and its environment, we transformed each variable into eight, multi-scale covariates. Continuous variables were transformed using neighbourhood statistics in ArcGIS. Using circular windows around camera stations, we calculated focal mean and standard deviation for each scale (window radius = 250 m, 500 m, 1 km, 2 km, 4 km, 8 km, 16 km and 32 km). Multi-scale categorical variables were generated via moving window analyses in FRAGSTATS. All rasters were standardized to 250-m resolution.

2.3 | Data analysis

In Step 1 of the multi-scale modelling approach, we identified the optimal scale and functional form (linear or quadratic) for all species–environment relationships via univariate generalized linear mixed-effects models (GLMMs; 'lme4' package (Bates, Maechler, Bolker, & Walker, 2015)) in R 3.3.2 (R Core Team, 2016). We included camera effort (i.e., total active nights per camera trap) as a fixed effect and sampling location nested within country as random effects. We selected best-supported scales and functional forms for each variable based on Akaike's information criterion, adjusted for small sample size (AICc; Burnham & Anderson, 2002). We note that the 13 original variables were selected based on careful a priori considerations of ecological importance. Subsequent transformations (e.g., linear vs. quadratic, small vs. large scales) simply provide enhanced understanding of *how* clouded leopards interact with variables of known importance. Once a given set of variables is chosen, all combinations and scales of those variables are implicit in the hypothesis space, even if they are not directly tested by an investigator. For rare species, the specific nature of ecological interactions is often unknown. Thus, testing a limited number of a priori 'best-guess' hypotheses at best provides limited scope and insight into complex relationships, and at worst is easily corrupted by investigator bias. Data-driven approaches that identify best-supported relationships by more fully interrogating the true complexity of the underlying hypothesis space can provide a more objective understanding of species–habitat relationships.

We then applied four filtering steps to reduce the number of variables included in the multivariate model (Table S3). (a) Twelve variables were removed that occurred at <10% of camera stations. Lack of representation of these habitat types at sampling locations resulted in insufficient data to reliably test their influence on clouded leopard detections. (b) AIC model selection identifies the best model relative to a chosen set of models, but it does not provide information on strength of relationship or effect size. Therefore, we also evaluated model performance of the top univariate GLMM selected for each variable and further required that optimal models identified via AIC also demonstrated strong evidence of relationship with the response variable (Macdonald,

Bothwell, et al., 2018; Šímová et al., 2011). It is possible for univariate relationships to exhibit non-significant marginal explanatory power, yet variables may become significant when considered conditionally in a multivariate model. Therefore, we chose a conservative threshold ($R^2 > 0.1$; $p < 0.05$) to eliminate only those variables exhibiting very weak relationships; three variables were eliminated. (c) Eighteen variables were removed after assessing multicollinearity ($|r| > 0.7$). For correlated pairs, we retained the variable with the lower AIC score, which therefore described a stronger relationship with the detection data. Finally, (4) we removed four variables with variance inflation factors (VIFs) ≥ 3 (Zuur, Ieno, & Elphick, 2010). Following filtering, nine variables were retained for the multivariate GLMM (Table 2).

To understand how *N. nebulosa* utilizes its environment, we modelled total number of independent observation (i.e., detection counts separated by at least one hour) as a function of scale-optimized covariates using a multivariate GLMM with the Poisson function. We included number of active trap nights for each camera station as a fixed effect and sampling location nested within country as random effects. This study's dense camera network was designed for estimating spatial capture–recapture density of mobile and territorial carnivores; hence, it violates key assumptions of occupancy modelling (e.g., closure, independence). We do not estimate occupancy probability here, but rather chose to use GLMM to assess relative habitat suitability, given its more flexible model assumptions. Although cameras were deployed in Vietnam, no clouded leopards were detected there. Among all countries involved in the Second Indochina War (i.e., Vietnam War), Vietnam sustained the heaviest impacts. Large-scale chemical defoliation and military combat resulted in mass deforestation and mortality of local wildlife. Subsequent opening of Vietnam to international markets exacerbated these impacts as rapid rates of post-war development and market-driven deforestation sustained high rates of wildlife loss, in contrast to other countries also impacted by the war (e.g., Cambodia,

Laos) but lacking international market access (Dudley, Ginsberg, Plumptre, Hart, & Campos, 2002). Non-detection at our Vietnam sampling location likely reflects unique historical, political and socioeconomic pressures not accounted for in our model rather than poor habitat suitability; therefore, we excluded Vietnam from the model building process. We ranked candidate GLMMs according to ΔAIC values and Akaike's model weight (w_i; Burnham & Anderson, 2002), and considered only models with ΔAIC ≤2 for model averaging ('MuMIn' R package, Barton, 2016). Additionally, we performed a multivariate environmental similarity surface (MESS; Elith, Kearney, & Phillips, 2010) analysis to provide an index of similarity between environmental space at our sampling locations used for model training and the model projection across Southeast Asia ('dismo' R package, Hijmans, Phillips, Leathwick, & Elith, 2012).

To enhance the utility of our model for policymakers and conservation practitioners, we reclassified the continuous predicted model using a range of stringent to moderate thresholds (97.5th, 90th, 70th and 50th percentiles) of habitat suitability. Thresholding the continuous model facilitated additional assessment of differences among countries in habitat quality, configuration, and extent, thereby providing a range of quantitative outputs to assist various management decisions. Using FRAGSTATS, we calculated eight landscape-level statistics for each habitat quality class and country: percentage suitable habitat (PLAND), number of patches (NP), patch density (PD), largest patch index (LPI; percentage of the total landscape comprised by the largest patch), area-weighted mean patch size (AREA_AM; larger patches contribute greater weight to the global mean), correlation length (GYRATE_AM), aggregation index (AI; level of clustering of like habitat classes) and total class area (CA). Multivariate relationships among nations were visualized using principal components analysis (PCA), and polythetic agglomerative hierarchical clustering (McGarigal, Stafford, & Cushman, 2000) on a Euclidean distance matrix, with Ward's fusion. The latter iteratively maximizes homogeneity within clusters with each successive clustering cycle,

TABLE 2 Multi-scale GLMM predicting *N. nebulosa* detections throughout mainland Southeast Asia, including the optimal scale for each covariate, AIC importance, standardized regression coefficients (β), adjusted standard error, z-scores and significance

Fixed effects	Optimal scale (m)	AIC imp.	β	Adjusted SE β	z	p
(Intercept)			−1.7532	0.1367	12.829	<0.0001
Camera effort (# trap nights)			0.2244	0.0132	16.966	<0.0001
% Closed forest	16,000	1	0.6464	0.1017	6.354	<0.0001
Compound topographic index focal mean	500	1	−0.2569	0.0514	4.999	<0.0001
Mean annual precipitation focal mean	32,000	1	0.4000	0.0965	4.146	0.0002
% Mosaic	1,000	1	−0.3709	0.0925	4.012	<0.0001
Protected area correlation length	8,000	1	0.1937	0.0748	2.591	0.0096
Shrubland/grassland correlation length	16,000	1	0.2722	0.0619	4.398	<0.0001
Slope position SD	500	0.78	0.0702	0.0570	1.232	0.2180
Slope position focal mean	8,000	0.17	0.0027	0.0167	0.160	0.8732
% Forest cover	16,000	0.17	0.0073	0.0629	0.117	0.9070

while considering all variables simultaneously. Lastly, we identified the most important high-quality habitat patches based on area (>1,000 km^2) and quantified the proportion of each patch protected according to the UNEP-WCMC & IUCN World Database on Protected Areas (2017), thereby identifying critical gaps in protection and opportunities for improving habitat conservation networks.

3 | RESULTS

From 2,892 camera stations, 234,281 trap nights of combined sampling effort were achieved. Clouded leopards were detected at 543 (18.42%) camera stations and at 39/45 sampling sites, with an average of 79.47 (SE ± 1.37) trap nights across all camera stations (Table 1). Total detections/site ranged from 0 in Vietnam to 103 in Myanmar. Detection rates ranged from 0 to 0.44, with the highest rates occurring in Malaysia. Comparing detection rates across countries, Myanmar ($\bar{x}$ = 0.41), India ($\bar{x}$ = 0.38) and Malaysia ($\bar{x}$ = 0.28) exhibited the highest levels; Bhutan ($\bar{x}$ = 0.12) and Laos ($\bar{x}$ = 0.17) were intermediate; and Cambodia ($\bar{x}$ = 0.07), Nepal ($\bar{x}$ = 0.08), Thailand ($\bar{x}$ = 0.10) and Vietnam ($\bar{x}$ = 0.00) had low detection rates (Table 1).

3.1 | Scale optimization

As predicted, given their relatively large home ranges (Austin, Tewes, Grassman, & Silvy, 2007; Grassman, Tewes, Silvy, & Kreetiyutanont, 2005), N. nebulosa habitat use was best-supported at broad spatial scales for most variables. Variables related to forest and shrubland/grassland habitat were selected at the 16-km radius focal landscape (% closed forest, % tree cover, shrubland/grassland extent). Additionally, mean annual precipitation (MAP), which influences vegetation density and biomass, was selected at the 32-km radius scale. Protected area correlation length (i.e., extent) and mean slope position were best-supported at the 8-km radius scale. Fine-scale relationships included mean compound topographic index (CTI; 500-m radius) and percentage mosaic habitat (1-km radius). Furthermore, quadratic relationships were best-supported for all variables except mean MAP and shrubland/grassland extent.

3.2 | Multi-scale model selection and validation

AIC model selection produced four top models with ΔAICc ≤2 (Table S4); model averaging then identified a final model with six variables (Table 2). Percentage closed forest was the strongest predictor of N. nebulosa detections (16-km radius focal landscape). When closed forest habitat increased from 65 to 100% of the landscape, we observed ~25% increase in detections (Figure 1a). MAP was also strongly, positively correlated with detections (32-km radius). Regions receiving <170 cm MAP were associated with low detection frequencies (<0.12); however, as precipitation increased above 170 cm, we observed a steady increase in detections (Figure 1b). Shrubland/grassland extent was also positively associated with N. nebulosa detections (16-km radius). Detection frequencies roughly

doubled (0.17 to 0.38) when shrubland/grassland extent within a 16-km radius focal window increased from 2 to 10 km (Figure 1c). Broad extent of protected areas was also positively associated with increasing detections (8-km radius). Variables negatively associated with N. nebulosa detection frequency included percentage mosaic habitat (1-km radius) and mean CTI (500-m radius; Figure 1d).

Using MESS analysis, we identified geographic locations with environments falling outside the range occurring at sampling locations used for model training, thus representing extrapolation (Figure S2a). Due to the cost of setting up and maintaining camera grids, and the challenge of detecting the rare and notoriously illusive N. nebulosa, limited resources necessitated placing cameras where there was some chance of detecting the species. While sampling locations were biased towards protected areas, locations were specifically chosen to maximize variation encountered by N. nebulosa across its range throughout Southeast Asia. Overall, multivariate environmental space at training data locations was highly similar to conditions encountered throughout the core of N. nebulosa's range (Figure S2a). Non-analog environments were identified along the species' range margins, where training data were more limited. Univariate similarity assessments revealed that lack of closed forest and high CTI were the strongest drivers of dissimilarity in central and south-western China, India, Bangladesh, and central Thailand. Very high precipitation along the western coastal lowlands of Myanmar and lower precipitation in central and south-western China also contribute to non-analog environments (Figure S2b). Model inference should be considered cautiously in these regions.

3.3 | Regional variation

The projected model revealed that 9.44% of the Southeast Asian landscape is highly suitable for N. nebulosa (Figure 2; representing top 10% of pixels), yet this varies substantially among countries (Figure S1). Neofelis nebulosa's core distribution coincides with Laos, Malaysia, and Myanmar, with 52.5%, 35.4%, and 30.7% of their landscapes harbouring highly suitable habitat, respectively. These countries also boast the largest mean patch sizes, greatest contiguous patch extensiveness and highest patch densities—highlighting their importance for clouded leopard conservation (Table 3). Considering total high-quality habitat area, India (64,897 km^2), Vietnam (43,078 km^2) and Thailand (35,727 km^2) also harbour substantial high-quality N. nebulosa habitat, in addition to the core highly suitable habitat available in Myanmar (205,008 km^2), Laos (120,631 km^2) and Malaysia (46,316 km^2). Bangladesh, Bhutan, Cambodia and Nepal are coincident with edges of N. nebulosa's distribution and are generally characterized by limited area and extent of high-quality habitat (Table 3, Figure S5).

We summarized multivariate habitat configuration and extent relationships among nations via PCA (Figure S3a–c). The first three axes collectively explain 88.5% of total variance among metrics (Table S6). PC1 is strongly aligned with percentage and extensiveness of high-quality habitat (≥90th percentile). Laos and Myanmar, followed by Malaysia, Bhutan and India, are characterized by high

values (Figure S3a); conversely, Bangladesh, China, Nepal, Cambodia and Thailand exhibit low percentage and extensiveness of high-quality habitat. Along PC2, China and Myanmar have the greatest extensiveness of medium- to high-quality habitat (≥50th percentile). Interestingly, China is an outlier, with a low- to high-quality habitat extent, but given its vast size, the highest area of medium- to high-quality habitat.

The cluster dendrogram shows strong partitioning into five hierarchical groups (Figure 3): (a) India, Vietnam, Bhutan and Malaysia; (b) Myanmar and Laos; (c) China; (d) Nepal; and (e) Bangladesh, Cambodia and Thailand. Univariate discriminant analyses revealed that correlation length of high-quality habitat (≥90th percentile) had the best ability to discriminate among clusters (Table S7), suggesting this metric can be a simple way to compare habitat patterns among countries. A bar plot of correlation length shows clear differentiation among countries and is highly consistent with the dendrogram clusters identified above (Figure 4). Additionally, we quantified the summed pixel values of predicted habitat suitability for each nation to provide a simple, intuitive and non-threshold-based comparison. This metric similarly ranks Myanmar and Laos well above the other nations in total predicted habitat suitability (Figure S4).

To assist with prioritization of habitat patches for conservation management, we identified the top 28 patches >1,000 km^2, ranked by descending high-quality habitat area (Figure 5; Table S8). The largest patch (1) extends throughout Laos and western Vietnam, and is 1.8 × larger than the next largest patch. We also identified Myanmar as a critical hub of *N. nebulosa* habitat; harbouring four of the top six patches (2, 3, 4, 6), these together cover 1.5 × the area of Patch 1. The 5th largest patch also identifies important habitat in Malaysia for future conservation focus. Assessing overlap between the top patches and protected areas (Figure 6, Table S8), we found that patches range from 0 to 98.32% protected ($\bar{x}$ = 43.29% ± *SE* 6.33%), although area protected drops to 31.46% when considering total habitat area throughout Southeast Asia. In contrast, 43.44% of high-quality *N. diardi* habitat on Sumatra, and 21.08% on Borneo are protected. Figure 6 illustrates three important points. First, high-quality habitat (brown) lacking protection (green) highlights core habitat potentially at risk of loss. Second, protected areas that do not currently intersect with high-quality *N. nebulosa* habitat may offer opportunities to expand clouded leopard habitat through restoration. Third, we identify three major gaps between core habitat patches. A denotes a vital triangle at the heart of *N. nebulosa*'s range. While a network of protected areas connects Laos in the east with the major southern axis of *N. nebulosa*'s range through northern Thailand and southern Myanmar, there is a conspicuous absence of protected areas connecting these two core regions to the second largest patch in northern Myanmar. Similarly, protected areas are lacking between Patch 2 and Patch 3 in western Myanmar (B), and
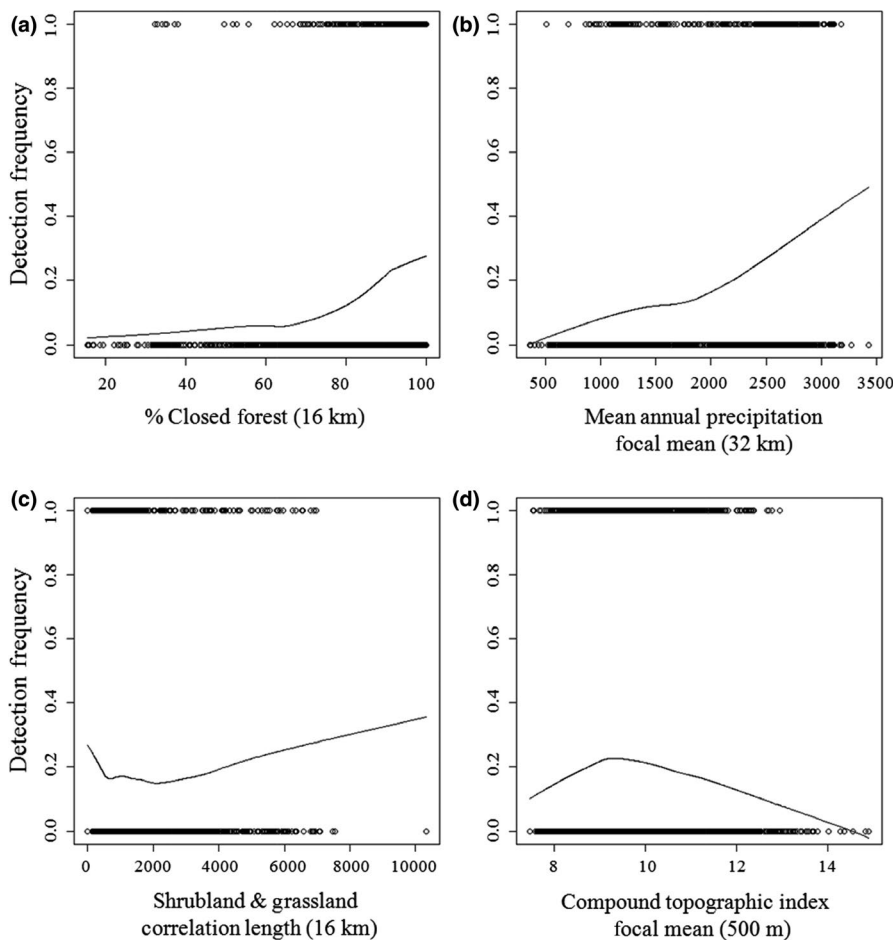

FIGURE 1 (a) Clouded leopard detection frequency increased ~25% when closed-canopy forest increased from 65 to 100% of the landscape. Detection frequency was positively associated with (b) increasing MAP and (c) increasing shrubland/grassland extent. (d) Detections were highest in landscapes with ~9.5 CTI and declined with both higher elevation ridges and lower elevation drainages
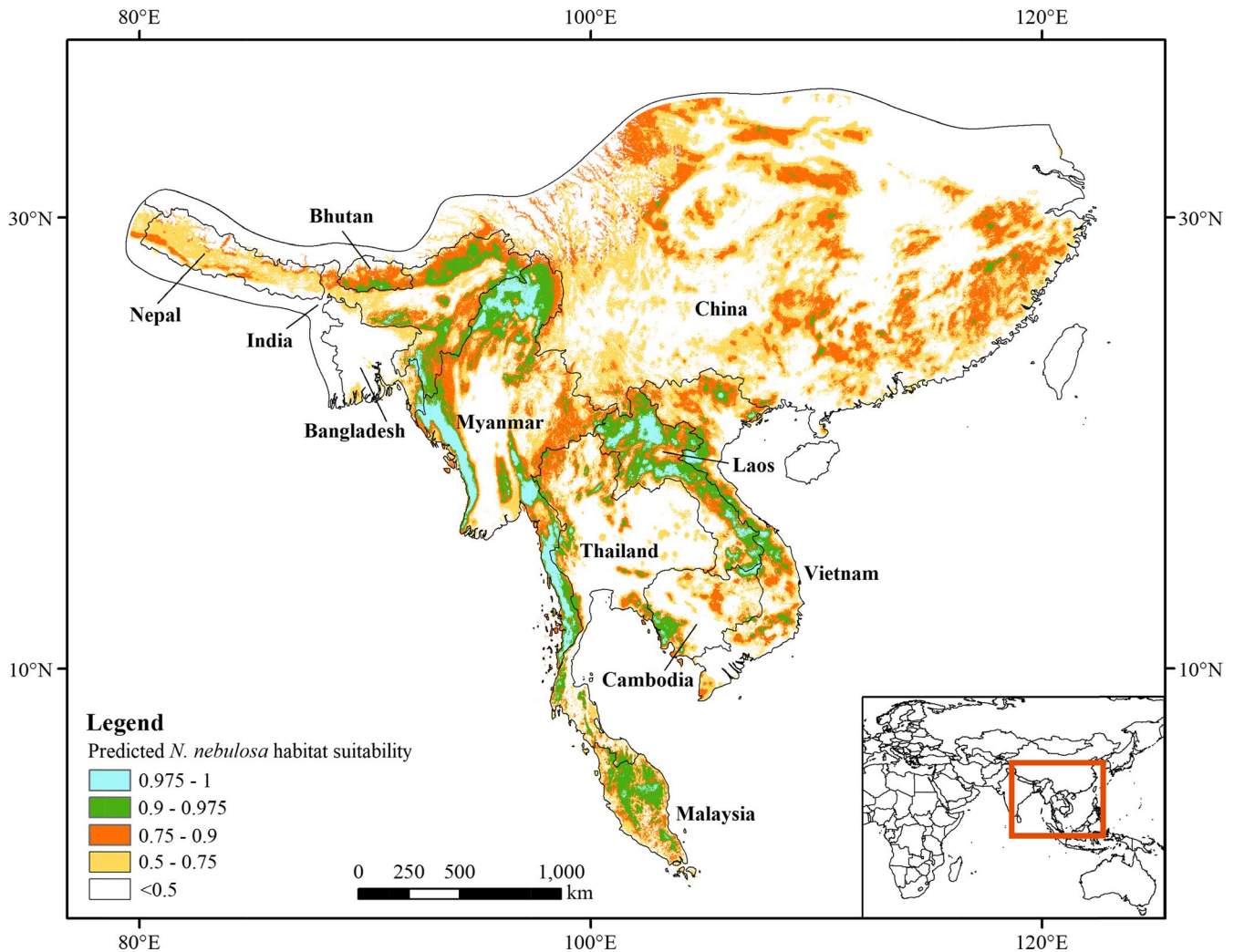
FIGURE 2 Predicted *N. nebulosa* habitat suitability across Southeast Asia, showing 50th, 75th, 90th and 97.5th percentiles of habitat suitability

between Malaysian Patch 5 and the rest of *N. nebulosa*'s range to the north (C).

4 | DISCUSSION

This study presents one of the few examples of scale-optimized species distribution modelling, and the only example we are aware of across the full range of a large carnivore. Using the largest clouded leopard camera trap survey ever conducted, spanning *N. nebulosa*'s full range across South and Southeast Asia, we demonstrate how multi-scale modelling can be used to identify primary habitat requirements, limiting factors and the spatial scales at which organisms are most strongly associated with key habitat components. Our projected model provides crucial information to assist conservation management, including the identification of highly suitable core habitat and medium-quality habitat likely critical to clouded leopard meta-population viability through its provisioning of essential connectivity corridors for dispersal and mating among core

populations. This is also the first empirically based comparative assessment of environmental niche space of two keystone, Southeast Asian carnivores.

4.1 | Niche comparisons

Using the same modelling approach as Macdonald, Bothwell, et al. (2018) allowed us to compare habitat models between the mainland clouded leopard and its allopatrically distributed sister species, the Sunda clouded leopard. We acknowledge that lack of data for prey availability and intra-guild competitive dynamics limit the utility of habitat models to accurately describe these species' realized niches. However, given that clouded leopards are threatened by rapid habitat loss, these models provide a timely assessment and represent the best models currently available for these species. Cross-model comparison identified many of the same variables and spatial scales as being important for both species, supporting model reproducibility and suggesting substantial niche conservatism at the genus level.

TABLE 3 Comparative analysis of landscape metrics for high-quality (≥90th percentile) and medium- to high-quality (≥50th percentile) thresholds of the projected model. ≥97.5th and 75th percentile analyses are presented in Table S5

| Country	% Suitable habitat	Number of patches	Patch density	Largest patch index	Mean patch size (km²)	Correlation length (km)	Aggregation index	Total class area (km²)
High-quality habitat								
Bangladesh	4.37	71	0.001	3.02	3,364	28	97.72	6,016
Bhutan	15.40	276	0.007	12.82	4,317	40	94.92	6,134
Cambodia	9.75	370	0.002	5.89	7,473	36	97.69	17,714
China	0.40	1,496	0.001	0.06	597	11	89.64	12,507
India	16.02	1,934	0.005	5.28	11,905	61	95.30	64,897
Laos	52.49	1,715	0.008	47.04	97,309	224	97.43	120,631
Malaysia	35.37	891	0.007	25.29	24,407	70	97.27	46,316
Myanmar	30.74	3,793	0.006	11.22	54,536	154	97.68	205,008
Nepal	0.02	32	0.000	0.00	3	1	67.13	24
Thailand	6.97	1,376	0.003	0.95	2,155	22	94.74	35,727
Vietnam	13.25	1,140	0.004	4.61	9,278	58	96.48	43,078
Total area	9.44	12,824	0.002	2.53	73,535	163	96.87	558,052
Medium- to high-quality habitat								
Bangladesh	23.83	2,261	0.016	11.51	9,501	45	94.43	32,823
Bhutan	76.15	25	0.001	76.12	30,322	92	99.03	30,337
Cambodia	44.05	2,544	0.014	19.15	25,521	79	96.36	80,096
China	40.14	32,659	0.011	28.83	645,062	505	96.29	1,239,918
India	54.54	2,625	0.007	51.18	194,730	235	97.74	220,882
Laos	88.55	950	0.004	87.58	199,164	261	99.15	203,584
Malaysia	84.24	623	0.005	82.10	104,844	146	98.20	110,375
Myanmar	71.22	5,292	0.008	68.84	443,884	397	98.50	475,038
Nepal	57.06	933	0.006	55.20	78,605	222	96.75	83,996
Thailand	37.24	6,104	0.012	18.74	51,495	110	96.27	190,759
Vietnam	65.53	3,330	0.010	50.80	132,281	276	97.60	212,762
Total area	48.95	59,091	0.010	39.41	1,885,800	789	97.15	2,880,569

Cluster dendrogram
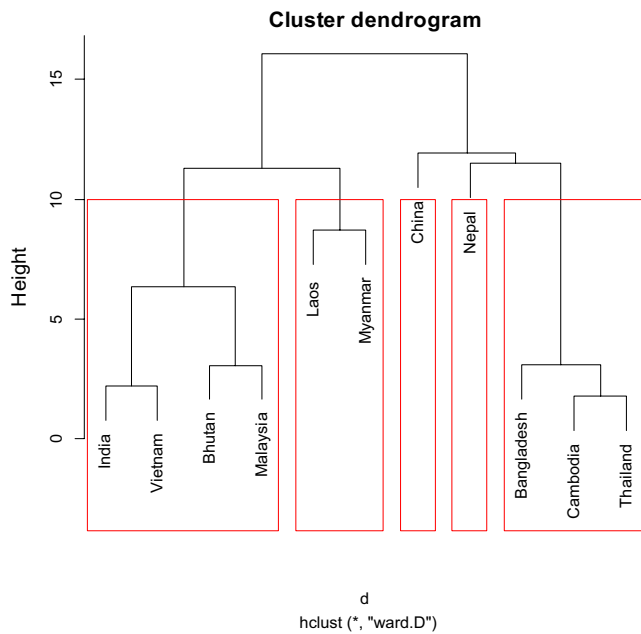
FIGURE 3 Cluster dendrogram illustrating differences in correlation length of high-quality *N. nebulosa* habitat among nations
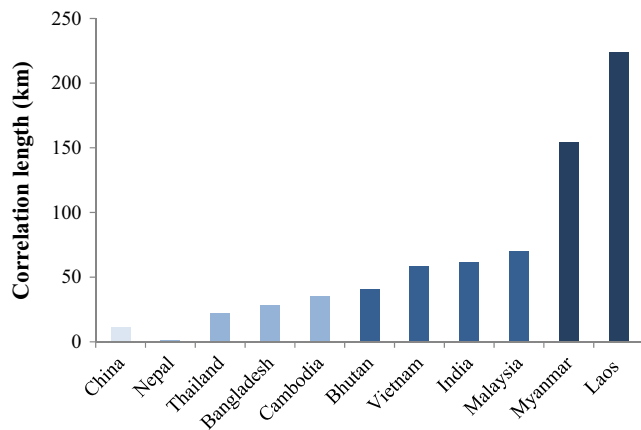

FIGURE 4 Correlation length of high-quality *N. nebulosa* habitat among nations. The four different clusters are indicated by different coloured bars

Closed-canopy forest was the strongest predictor of clouded leopard detection; few *N. nebulosa* were observed when the landscape was <65% closed forest. Furthermore, detections were most strongly correlated with forested landscapes at the 16-km radius scale, consistent with previous estimates of *N. diardi's* relatively broad-scale movements (Hearn et al., 2013; Hearn, Cushman, Ross et al., 2018). Both species are strongly associated with landscapes dominated by extensive forest cover at broad spatial scales. Both the mainland and Sunda models also showed strong negative associations with mosaic cropland habitat and large-scale plantations, respectively. Deforestation and agricultural intensification are clearly dire threats to clouded leopards. *Neofelis nebulosa* detections were also strongly, positively associated with increasing precipitation. Our

model suggests a threshold response; low detections were observed below 170 cm MAP and steadily increased above 170 cm. This association is particularly informative for predicting future climate change risks to clouded leopards. Regions that experience increasing aridity will have reduced capacity to support high-density forests, and by association, clouded leopards.

Although percentage availability of highly suitable habitat is comparable among mainland Southeast Asia (9.44%), Borneo (10.04%) and Sumatra (8.98%) (Macdonald, Bothwell, et al., 2018), average travel distance (correlation length) within contiguous, core habitat is much greater (163 km) for *N. nebulosa* than that available to *N. diardi* on Borneo (15 km) or Sumatra (44 km). Accordingly, *N. nebulosa* was most strongly associated with forest habitat at the 16-km radius scale, whereas *N. diardi* forest use was best-supported at the 10-km radius scale. Because 10-km radius was the largest scale investigated for *N. diardi*, the Sunda model was limited in its ability to determine whether larger spatial extents are similarly more important for *N. diardi*. The expanded scale investigation undertaken for *N. nebulosa* (up to 32-km radius) allowed us to determine that *N. nebulosa* detections were most strongly associated with contiguous forest tracts of at least 800 km^2 (16-km radius window; Table 2). While the difference in optimal scale may reflect less extensive habitat available to *N. diardi*, it may also reflect differences in prey availability, which is known to strongly influence habitat selection in clouded leopards (Mohamad et al., 2015).

Comparative analysis revealed another distinction between the *Neofelis* species with respect to shrubland/grassland habitat. Whereas the comparable lowland open land cover class was non-significant in the Sunda model, shrublands/grasslands were positively correlated with increasing *N. nebulosa* detection. We know of no studies of *N. diardi* utilizing this habitat type; however, Grassman et al. (2005) suggest *N. nebulosa* may use grasslands for hunting. Of note, this positive association with natural open habitats does not extend to anthropogenic forest clearings (e.g., plantations, croplands), suggesting behavioural differences in *N. nebulosa* response to natural versus human-induced forest fragmentation.

Our model suggests additional niche divergence with respect to compound topographic index. Although Sunda sampling locations occurred along a narrower elevation gradient (6–1,896 m) than mainland locations (128–4,496 m), we found that Sunda clouded leopard detections on average were associated with lower CTI than mainland clouded leopards. *Neofelis nebulosa* does occur in higher elevations (e.g., Bhutan, Nepal, China); however, these coincide with range edges. Declining detections in lower CTI regions may be due to both habitat preference and population dynamics typical of marginal populations (e.g., smaller effective population sizes, lower dispersal and mating potential) (Bothwell et al., 2017; Cushman et al., 2018; Eckert, Samis, & Lougheed, 2008). Divergence in optimal CTI may also reflect greater deforestation intensity in Borneo and Sumatra. Vast conversion to oil palm and acacia plantations within Indonesia and Malaysian Borneo may be driving *N. diardi* into the refuge of more remote highlands characterized by lower CTI.
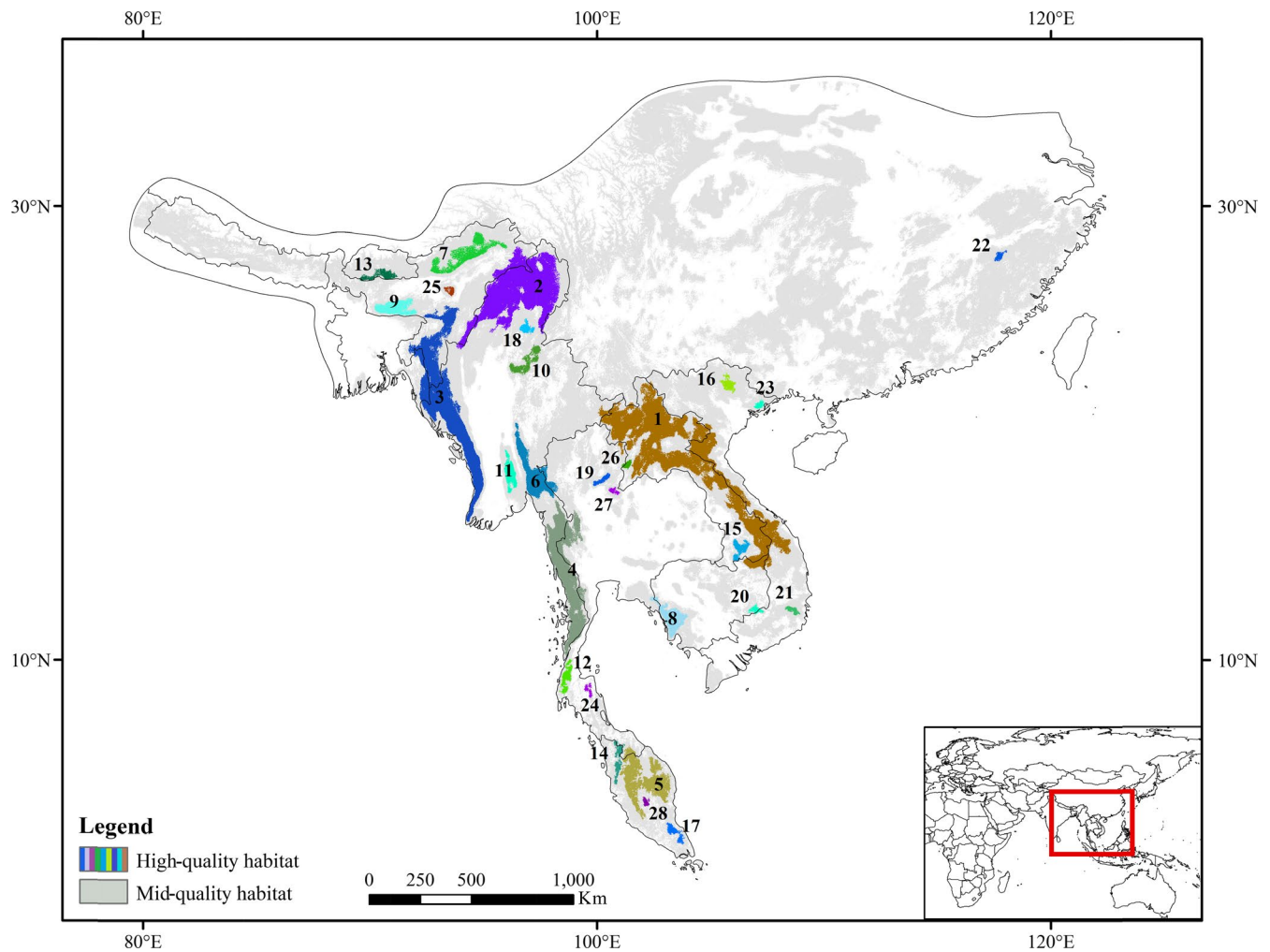
FIGURE 5 Top 28 patches of high-quality *N. nebulosa* habitat (≥90th percentile), ranked according to patch area. Largest patch = 1, smallest patch = 28. Area, correlation length, and conservation status of patches are presented in Table S8

4.2 | Future research needs

Clouded leopards co-occur with a varying guild of felids and prey species across their range. The habitat selection model developed here provides a timely assessment to support critical habitat conservation initiatives for a species facing rapid habitat loss; however, both intra-guild competitive dynamics and hunting opportunities are influential drivers of habitat selection for these carnivores (Mohamad et al., 2015). Detectability may be affected by larger felid trail use, as observed in other mammal communities (Harmsen, Foster, Silver, Ostro, & Doncaster, 2010). The distribution of and variation in prey species, including a wide variety of birds, squirrels, monkeys, deer and wild pigs, may contribute to a narrower realized niche than observed for the current habitat model. For example, we suspect the positive association of *N. nebulosa* with shrublands and grasslands may be driven by lower poaching intensity and greater prey opportunities in this habitat type on the mainland in contrast to *N. diardi* in the Sunda Islands. We are currently exploring both intra-guild competitive dynamics and associated community biodiversity patterns, which we expect will provide additional insights into clouded leopard habitat selection.

Additionally, poaching poses a critical threat to both species. Direct exploitation is particularly high in Laos (Johnson, 2012), Myanmar (Min, D'Cruze, & Macdonald, 2018) and Vietnam (Willcox, Tran, Hoang, & Nguyen, 2014), and poaching has been implicated in decreased abundance and density of *N. diardi* (Brodie et al., 2015; Hearn et al., 2017; Macdonald, Bothwell, et al., 2018) in the Sunda Islands. Although we recorded poacher presence for core WildCRU sites, these data were unavailable for collaborator surveys. Therefore, we lacked statistical power to directly assess poaching impact on *N. nebulosa*. However, poaching is clearly a major threat driving large mammal decline in the tropics (Benítez-López, Santini, Schipper, Busana, & Huijbregts, 2019). For example, lack of clouded leopard detections in Vietnam is consistent with similar findings for leopards (*P. pardus*; Rostro-García et al., 2016), tigers (*P. tigris*; Lynam & Nowell, 2011; Goodrich et al., 2015) and non-*Panthera* felids in this country (Willcox et al., 2014). Given that our study highlights the importance of large protected areas for clouded leopard conservation, it is possible that the small size of Vietnam's protected areas, coupled with habitat loss and poaching, may have exacerbated *Neofelis* extirpation there (Willcox et al., 2014). In Phnom Prich Wildlife Sanctuary,
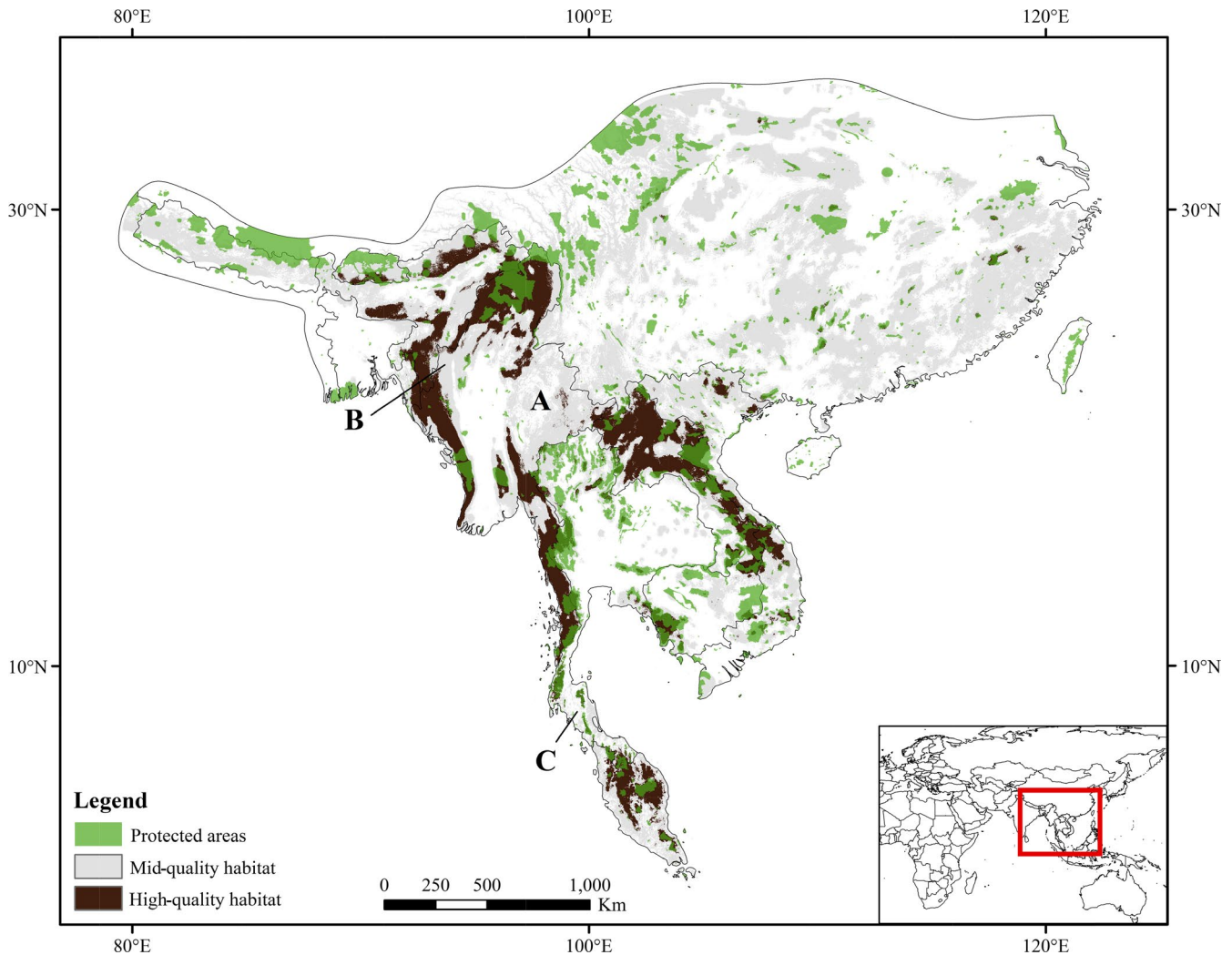
FIGURE 6 UNEP-WCMC & IUCN Protected Areas (2017) overlaid on the *N. nebulosa* multi-scale model. Uppercase letters indicate critical gaps in protection among key high-quality habitat patches

a core WildCRU site in eastern Cambodia, we likely recorded the last clouded leopard there in 2013; subsequent, extensive camera trap surveys at the same site in 2016 and 2018 failed to detect *N. nebulosa*. Clouded leopard densities in this region were likely low due to restriction to isolated, evergreen forest patches (Gray, Channa, Chanrattanak, & Sovanna, 2014), thus making this population especially prone to extirpation in the face of recent increases in illegal snaring. Illegal snaring has reached crisis levels in Southeast Asia (Gray et al., 2018); without intervention, further declines of clouded leopards in this region can be expected.

4.3 | Scale and conservation management planning

Multi-scale modelling provides an efficient means to optimize conservation management planning to the scales at which environmental variables impact species occurrence. For clouded leopards, this suggests the need for broad-scale, landscape-level reserve network design, with targets for forest cover >65% and a minimum 800 km² of highly suitable habitat. Our scale optimization

suggests a minimum 8 km buffer around protected areas should be managed for low coverage of plantations and mosaic cropland (Table 2). To assist in prioritizing continuing conservation efforts, we identified the top 28 high-quality habitat patches (Figure 6; Table S7) and highlight key gaps in protection and connectivity (Figure 6).

Three key recommendations emerged based on overlap between our habitat model and protected areas. First, large regions of high-quality habitat currently beyond protected areas may risk fragmentation. Regional development planning should avoid dissecting unprotected core habitat. Second, habitat restoration has the potential to improve *N. nebulosa* carrying capacity of less suitable habitat both within and beyond protected areas. For example, China harbours little high-quality habitat, yet boasts vast area and extensiveness of medium- to high-quality habitat. Economic and land use changes that allow for improved forest cover and wildlife protection have the potential to turn China into a restoration opportunity for *N. nebulosa*. China's target for planting 6.7 million hectares of trees in 2018 alone is grounds for cautious optimism (Cernansky, 2018).

Additionally, we identified three major gaps in protection between core habitat patches. Conservation efforts should prioritize the establishment of connectivity corridors linking Patch 1 and Patch 2 in northern Myanmar. In western Myanmar, additional corridors are needed to connect the second and third largest patches. Lastly, establishing protected corridors between Patch 5 and the rest of *N. nebulosa*'s range to the north is critical to mitigate inbreeding depression in Peninsular Malaysia.

Clouded leopards are widespread and adaptable. We detected *Neofelis* across diverse habitats from sea level up to ~4,500 m, yet dense forest emerged as a consistent, fundamental niche requirement. Both the Sunda and mainland models clearly demonstrate sharp declines in detections with forest loss. Continued efforts to preserve core, high-quality forested habitats and corridors connecting them are critical for the persistence of both species. These efforts are particularly important in Laos, Myanmar and Peninsular Malaysia, where the greatest area and extensiveness of high-quality *N. nebulosa* habitat occurs. Our findings urge both hope and caution. Clouded leopards face dire threats from increased poaching and land use changes that are rapidly reducing and fragmenting Southeast Asian forests. Our observation that at least one population of *N. nebulosa* in Cambodia has likely been extirpated during the period of our fieldwork raises the chilling premonition that even *N. nebulosa's* versatility may be no match to the attrition of poaching. Yet, our results, given habitat selection at broad spatial scales (>800 km^2), highlight clouded leopard's value as an ambassador for conservation of broader forest biodiversity (Macdonald et al., 2017), and support its capacity to act as an umbrella for the protection of co-occurring Southeast Asian species similarly threatened by widespread deforestation (Macdonald, Burnham, Hinks, & Wrangham, 2012; Macdonald et al., 2017; Roberge & Angelstam, 2004).

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA ACCESSIBILITY

All input GIS layers, the habitat suitability model and the high-quality habitat patch map are archived on Dryad. Given the extremely sensitive nature of clouded leopard occurrence data with respect to illegal wildlife trade, locations of camera traps will not be made public so as to avoid further endangering the species. However, we welcome correspondence with scholars and conservationists regarding collaborative use of the data to advance science and conservation of clouded leopards, their associated communities and habitats.

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BIOSKETCH

The team of authors is broadly interested in providing practical solutions for biodiversity conservation, and the improvement of statistical models for better understanding how environmental and anthropogenic factors influence the distribution and continued persistence of biological diversity. Wildlife Conservation Research Unit (WildCRU) webpage: https://www.wildcru.org.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.