Mid-sized felids threatened by habitat degradation in Southeast Asia

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A R T I C L E   I N F O

A B S T R A C T

Deforestation and poaching in Southeast Asia have driven a stark decline in the region's apex predators, including large felids like tigers and leopards. Meanwhile, some small felids thrive in the region's human-modified landscapes. The extent to which medium-sized felids cope with anthropogenic disturbances remains poorly understood, but this information is crucial for the conservation of threatened felids and key trophic interactions that maintain high-diversity food webs. Here, we use the largest camera-trap dataset from Southeast Asia to conduct a multi-scale synthesis of the habitat associations of two cryptic felids, the Near-Threatened Asiatic golden cat (*Catopuma temminckii*) and the Endangered bay cat (*Catopuma badia*). Unlike many mesopredators, both species exhibited poor tolerance to habitat degradation (i.e. selective logging, edges or fragmentation). The golden cat was positively associated with forest patch size and elevation, and negatively associated with degraded forests, and the bay cat was negatively associated with human population density. Our habitat suitability model suggests that ongoing forest fragmentation and degradation have critically reduced suitable habitat for the golden cat, giving reason to suspect a population decline that calls for a revision of the species' IUCN Red List status to Vulnerable. There is also evidence that the bay cat may be more widely distributed in Borneo than previously thought, including in areas currently threatened by deforestation. Our results indicate both species face a high risk of becoming extirpated from many of the region's remaining forests. In areas where apex predators have been extirpated, these charismatic mid-sized felids can become umbrella species to protect forests with high biodiversity value.

1. Introduction

Habitat loss and fragmentation is the most pressing threat to biodiversity in tropical forests (Haddad et al., 2015; Alroy, 2017). Anthropogenic disturbances further degrade the remaining natural habitat in human-modified landscapes (Alroy, 2017), and this disproportionately affects large carnivores with an extensive home range, low population density, and strong dependence on depleting prey populations (Ripple et al., 2014). By contrast, many smaller carnivores with flexible diets (typically mammalian mesopredators), persist or even become more abundant in fragments and degraded habitats because they have smaller home ranges, can adapt to changing foraging conditions (e.g. food subsidies near edges), and may benefit from decreasing competition and predation pressure from extirpated apex predators (Prugh et al., 2009).

Differential sensitivities to habitat degradation in mammalian carnivores can drive selective extirpation from a landscape (Crooks, 2002) and ultimately contribute to reshaping communities towards trophic downgrading (Estes et al., 2011; Filgueiras et al., 2021). Mesopredators therefore serve increasingly important ecological roles in degraded forests, in some cases filling niches previously occupied by extirpated apex predators (Prugh et al., 2009). These dynamics are especially important in Southeast Asia, which faces high rates of deforestation driven by land-use change (Wilcove et al., 2013; Margono et al., 2014) and where apex predator extirpations have given rise to unique species assemblages (Amir et al., 2022a). However, our understanding of mesopredator ecology in the region's degraded forests remains lacunary, especially regarding the ability of mid-sized felids to cope with habitat degradation. Are Southeast Asia's mid-sized cats thriving in degraded

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forests, or are they declining like their larger pantherine relatives?

Felids exhibit heterogenous responses to habitat degradation in Southeast Asia, which is home to the world's highest felid diversity (Luo et al., 2014) and is a designated high-priority area for felid conservation (Dickman et al., 2015; Luskin et al., 2017; Haidir et al., 2020a; Silmi et al., 2021; Amir et al., 2022a; Hendry et al., 2023). While some species depend on large, intact forests, and are particularly susceptible to deforestation, other felids appear to have more flexible habitat requirements, making them potentially tolerant to degraded habitats (Nowell and Jackson, 1996). For example, tigers are more abundant in larger intact forests than in smaller fragments, which are susceptible to edge effects and where they conflict with livestock and humans (Luskin et al., 2017), marbled cats avoid degraded forests with canopy gaps (Hendry et al., 2023), whereas leopard cats appear to thrive in oil palm plantations (Silmi et al., 2021). Other non-felid mid-sized carnivores in the region, such as the common palm civet, also adapt well to degraded, human-modified landscapes (Dehaudt et al., 2022), but this is not true for all civets (Dunn et al., 2022). Significant gaps remain in our understanding of small cat ecology, with a critical lack of data on rare and cryptic species. Very little is known of the effects of habitat fragmentation and degradation on two species of mid-sized cats, the Asiatic golden cat *Catopuma temminckii* (Vigors and Horsfield, 1827) (hereinafter referred to as 'golden cat' for convenience, not to be confused with the African golden cat *Caracal aurata*), and its Bornean relative the bay cat *Catopuma badia* (Gray, 1874) (Zanin et al., 2015).

The golden cat (8.5–16 kg) is found throughout mainland Southeast Asia and Sumatra and is believed to be a habitat generalist (Sunquist and Sunquist, 2002; Patel et al., 2016). Research on the golden cat's response to anthropogenic disturbance remains inconclusive, with some studies suggesting that it maintains higher occupancy in edges near recently deforested areas (Haidir et al., 2020b), others suggesting higher occupancy away from human settlements (Cremonesi et al., 2021), and others unable to identify significant predictors (Sunarto et al., 2015). Similarly, the Bornean endemic bay cat (2–4 kg), mainly confined to inland dipterocarp forests, is believed to occupy areas of low fragmentation and low human footprint (Hearn et al., 2016b; Hearn et al., 2018), but it has been observed in logged and degraded forests (Kitchener et al., 2004; Wearn et al., 2013; Mathai et al., 2014; Sastramidjaja et al., 2015; Hearn et al., 2018; Mohd-Azlan et al., 2019), and its tolerance to degraded habitat and human disturbance remains unknown. The golden cat and the bay cat are believed to be experiencing substantial population declines concomitant with habitat loss, and are listed by the IUCN, respectively, as Near Threatened but 'very close' to Vulnerable, and Endangered (McCarthy et al., 2015a; Hearn et al., 2016a). The paucity of available information on the habitat associations of these highly elusive felids is problematic, as it hinders assessments of their population status (McCarthy et al., 2015a; Hearn et al., 2016a) in the fragmentated and degraded forests that now dominate the region's remaining natural habitat. The bay cat, in particular, has long been considered the world's least known felid (Sunquist and Sunquist, 2002).

The proliferation of camera-trapping data presents a remarkable opportunity to improve our knowledge of these cryptic felids' ecology, but robust conclusions are difficult to draw from isolated studies. We overcome this difficulty by collating the largest (to our knowledge) dataset of *Catopuma* occurrence records, combining data from published reports and new camera-trapping surveys conducted in 10 landscapes, to provide the most comprehensive and up-to-date account of habitat associations for the golden cat and the bay cat. As patterns of habitat selection and use vary at different spatial scales (Gaillard et al., 2010), we investigated relationships between *Catopuma* occurrence and key indicators of habitat degradation and anthropogenic disturbance both at the regional scale across landscapes (with variables homogenised within a 20-km radius) and at the local scale within landscapes (within a 1-km radius). We also used MaxEnt distribution modelling to map predicted suitable habitat remaining within each species' range, to investigate patterns of habitat degradation linked with potential population decline.

Our main objective was to evaluate our species' tolerance to forest fragmentation and degradation, to determine whether they can persist or even thrive in human-modified landscapes, or risk sharing the fate of their larger felid relatives extirpated from many of Southeast Asia's remaining forests.

2. Methods

2.1. Data collection

We compiled presence and absence data for the golden cat and the bay cat from four sources: (1) published reports of camera-trapping studies; (2) new camera-trapping surveys conducted across the study region; (3) the Global Biodiversity Information Facility database (GBIF Secretariat, 2021), a global repository of biodiversity data including museum records and citizen science reports; and, for the bay cat, (4) published reports from the Borneo Carnivore Database (Hearn et al., 2016b). Presence data consists of georeferenced occurrence records. We defined a camera-trapping study as a continuous sampling effort using at least 5 cameras within a landscape (10–1000 km^2). We refer to the sampling area as a 'landscape' – usually a national park, a production forest, or a network of forest fragments within a 100 km^2 area. We collated data from a total of 128 camera-trapping studies, including 24 new camera-trapping surveys (Fig. 1).

We located published camera-trap records by searching Web of Science with the following criteria: "camera trap*" and Asia* or Thai* or Malaysia* or Indonesia* or Singapore* or Borneo* or Cambodia* or Vietnam* or Lao* or Myanmar* or Burm* or Sumatra* or Borne*. We selected from the returned list of studies those that were written in English and reported relevant results for the species of interest, including location, sampling effort (number of cameras, and deployment length or total trap nights), and number of independent captures (generally defined based on a 30–60 min interval between captures of the same species). We examined the references provided in key papers to identify and include further sources. For each study, we also recorded a variety of relevant covariates.

In addition, we conducted 24 new camera-trapping surveys in 10 landscapes in Thailand, Peninsular Malaysia, Singapore, Sumatra, and Malaysian Borneo between December 2013 and March 2020 (see Table A3 for landscape characteristics). We standardised deployment methods across all landscapes and set between 18 and 78 passive infrared camera traps across each sampling area. Cameras were placed within a systematic grid and spaced at least 500 m apart in large, forested landscapes (> 50 km^2) and 100–500 m apart in smaller forest patches, attached to trees 0.3 m above ground along hiking trails or natural wildlife trails, and deployed for 60–90 days. We considered captures independent if they occurred at least 30 min apart. We produced detection history matrices containing detection/non-detection data for each sampling occasion (1 = species detected; 0 = species not detected; NA = inactive sampling unit or occasion).

2.2. Analysis of regional-scale habitat associations

First, we investigated relationships between the number of captures in published studies and new camera-trapping surveys and key indicators of habitat degradation and anthropogenic disturbance across landscapes using generalised linear mixed models (GLMMs). We treated captures as count data and tested reduced model fit with Poisson, zero-inflated Poisson, and negative binomial distributions. Models included effort as a fixed effect and landscape as a random effect, as effort varied between studies and several landscapes were surveyed on multiple occasions. We chose to use the raw count data as opposed to a relative abundance index (RAI, usually the number of independent captures per 100 trap nights) following Ash et al. (2020), noting that these approaches do not account for variation in detection probability and thus may not reflect true abundance (Sollmann et al., 2013). Therefore, in
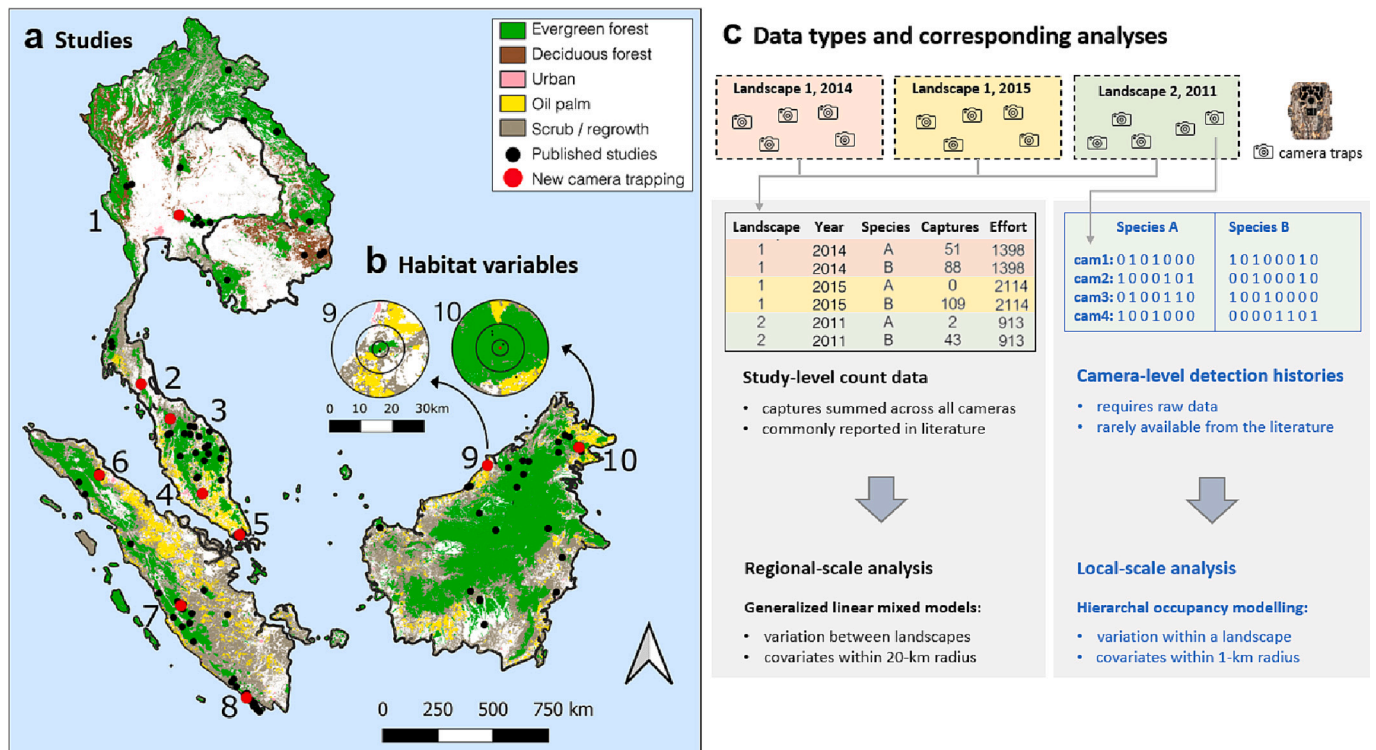
Fig. 1. Study area and diagram of camera-trapping data types and analyses. (a) Landscapes where camera trapping was undertaken, with black circles showing the location of published camera-trapping studies and red circles showing locations of new camera-trapping surveys conducted by the Ecological Cascades Lab program, including Pasoh data from the Tropical Ecology Assessment and Monitoring Network. The map inset (b) shows the process of extracting habitat covariates: for regional-scale analyses, landscape characteristics were averaged within a 20-km radius around the landscape centroid; for local-scale occupancy analyses within landscapes, covariates were averaged within a 1-km radius around each camera. Panel (c) shows the structure of our different datasets and the different types of analyses used: on the left side, the study-level species counts per landscape, used for regional-scale analysis; on the right side, the camera-level detection histories, used for hierarchical occupancy modelling. For convenience, Myanmar and Vietnam are not shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

this analysis, we are implicitly assuming that detection probability does not vary between published studies and acknowledge that this may introduce measurement error. We also acknowledge that there is unexplained variation in captures owing to slight differences in equipment and deployment methodology between the published studies. Both sources of measurement error likely reduce our statistical power and impact our ability to detect actual relationships.

In addition to biophysical descriptors (latitude, annual precipitation, average elevation), we tested the effect of six indicators of habitat degradation and anthropogenic impact: forest patch size, percentage of forest cover, forest landscape integrity index as defined by Grantham et al. (2020), human population density, night light intensity, and the human footprint index as defined by Venter et al. (2016). Our covariates values were derived from GIS layers and describe the area within a 20-km radius around the centroid of each landscape. We used this vast study area (1256 km^2) to account for some large camera-trapping grids and the possibility of low precision in the centroid coordinates provided in or inferred from the landscape description in some studies. Sources for each GIS layer and the year of their measurement are summarised in Table A4.

We developed univariate linear and non-linear (quadratic) models and filtered out non-significant ($p > 0.05$) and highly correlated ($| r | > 0.6$) variables before testing multivariate additive linear models. We used AIC model selection to identify the most parsimonious models. GLMMs were implemented using the R package 'lme4' (Bates et al., 2015).

2.3. Analysis of local-scale habitat associations

We assessed the effect of habitat variables on golden cat occupancy at the local scale within landscapes, using single-species occupancy modelling with data from our new camera-trapping surveys. To account for imperfect detection, occupancy modelling uses a repeated bootstrap procedure to estimate the species' probability of presence at a site (Ψ) (MacKenzie et al., 2002). We conducted this analysis for the golden cat only, as our new camera-trapping surveys did not yield enough bay cat captures to provide robust model results (see Table A5 for details of sampling effort, as well as capture rates and naïve occupancy for both species). We limited our sampling occasions to 90 days to satisfy the requirement of population closure (Rovero and Spitale, 2016). For modelling purposes, we collapsed sampling occasions into 5-day intervals to increase detection probability while maximising model fit (Rovero and Spitale, 2016) and we retained this value after testing incrementally longer intervals. To satisfy the requirement of spatial independence, we resampled the data spatially into 3.46 km^2 hexagonal grid cells with an apothem of 1 km, defined as our sampling units. When multiple cameras fell within the same grid cell, we aggregated captures to produce a single detection history and averaged covariate values, as suggested by Darmaraj and Linkie (2020). We included survey as a fixed effect to maintain the spatial and temporal independence of our sampling units and satisfy the assumption of population closure in the models. In addition to the variables described previously, we tested the effect of local-scale indicators of habitat degradation and disturbance. We calculated distance to forest edge, percentage of oil palm plantation cover, percentage of forest loss (between 2000 and 2019), and percentage of degraded forest, within a 1-km radius around the centroid of

the sampling unit. We developed univariate models and filtered out non-significant ($p > 0.05$) and highly correlated ($| r | > 0.6$) variables before testing multivariate additive models. We used AIC model selection to identify the most parsimonious models. Occupancy models were implemented using the R package 'unmarked' (Fiske and Chandler, 2011) (Fig. 1).

2.4. Mapping of extent of occurrence and suitable habitat

Finally, to determine the accuracy of currently available representations of our species' range, we calculated their extent of occurrence (EOO) in km^2 based on the relevant IUCN Red List range maps (McCarthy et al., 2015a; Hearn et al., 2016a), and compared it to our own estimate of the area of remaining forest within that range, based on remote-sensing forest cover data from 2015 by Miettinen et al. (2016). As all remaining forest patches may not be occupied, this updated EOO is conservative and should be interpreted as an estimate of the remaining available habitat. We also calculated the percentage of protected areas within each species' range, based on geographical data obtained from the IUCN World Database on Protected Areas (UNEP-WCMC and IUCN, 2021).

To obtain a high-resolution representation of variation in habitat suitability within our species' updated EOO in the study region, we generated a species distribution model using MaxEnt (Phillips et al., 2006), based on presence-only data and relevant spatial variables. Models based on presence-only data are reliable but less precise than occupancy-based distribution models accounting for imperfect detection and spatial autocorrelation (Johnson et al., 2013), but this latter approach could not be implemented in the absence of sufficient camera-level detection histories, which are not readily available in published studies. Instead, we used our combined dataset of landscape-level occurrence records, removing records predating 2000 where possible to avoid including false positives in areas where the species may no longer be present. Our environmental layers included both biogeographical factors (mean annual rainfall, elevation, land cover type), as well as indicators of anthropogenic impact (percentage of forest cover, forest landscape integrity index, distance to edge, oil palm cover, human population density, and nightlights) (Table A4). We report the output of an averaged model generated through a 10-replicate cross-validation, and the results of a Jackknife test estimating the relative contribution of each predictor to the averaged model. We assessed model performance using receiver operating characteristic (ROC) analysis. We chose a transformed complementary log-log output format to generate a map of the estimated probability of presence for our species across the region. We then generated final maps in QGIS, showing each species' probability of presence in the study region. We clipped the MaxEnt output layer to the forest cover layer and to the IUCN range layer in order to show predicted habitat suitability in our updated EOO (i.e. remaining forest within the IUCN range) (Fig. 4.e). For the bay cat, since a number of occurrence records were located outside the species' IUCN range, we showed predicted habitat suitability in remaining forests across the entire island of Borneo (Fig. 5.c).

2.5. Advantages and limitations of multiple methods

MaxEnt and GLMMs are two methods used to analyze the occurrence and relative abundance of species, respectively. MaxEnt uses presence-only records to map the probability of occurrence, with equal weighting given to presences at high and low densities. Any occurrence record, even roadkill or citizen science uploads, can be used in MaxEnt, resulting in a larger effective sampling area than methods requiring targeted sampling. MaxEnt is useful for identifying environmental covariates associated with species presence, including those associated with low densities or population sink areas. Camera trap detection rates, often used as a proxy for relative abundance or species activity level, have advantages and drawbacks compared to presence-only SDMs such

as MaxEnt. GLMMs can differentiate the quality of occupied areas but require targeted fieldwork, resulting in a smaller effective sampling area compared to MaxEnt SDMs. We opt for the complementary use of both approaches, with SDMs ideally suited to mapping suitable habitats at regional scales, while GLMMs are better at identifying landscapes or covariates with high abundance or activity (e.g. potentially population sources).

Our use of MaxEnt and GLMMs has important assumptions that may not be met in our dataset. First, we assume that detections are 'the consequence of random or representative sampling and that detectability during sampling does not vary with the covariates that determine occurrence probability' (Yackulic et al., 2013). In efforts to reduce bias associated with variation in detectability, we limited our study area to regions with predominantly evergreen tropical forests and we note that most detections of both species came from camera traps targeting predators. However, one could imagine that cameras placed in remote primary-forest national parks may use a limited number of defined hiking trails where there is high felid traffic, compared with surveys in degraded forests (e.g. logged or small fragments) where cameras are placed along more numerous smaller trails with lower felid traffic. We do not account for the latter issues in MaxEnt or GLMMs, however, we do address detection probability in our local scale hierarchical occupancy modelling. Given the comparatively limited coverage of camera surveys with raw capture histories that could be included in the hierarchical occupancy modelling, the results should be interpreted as 'local-scale' (variation within a landscape), and would be unsuitable for projections across the region.

3. Results

We collated capture lists from a total of 128 camera-trapping studies from across Southeast Asia, including new camera-trapping surveys (97 and 31 studies from the golden cat's and the bay cat's respective regions of occurrence). Combined with GBIF data and other sources, our dataset contains a total of 53 presence records for the golden cat, and 62 presence records for the bay cat (Table A1).

Our new camera trapping yielded 31 independent golden cat captures and 2 independent bay cat captures. Within the golden cat's region of occurrence, we deployed a total of 1066 cameras in 7 landscapes for 58,929 trap nights. We detected the species in all landscapes surveyed in Sumatra as well as in Ulu Muda in Peninsular Malaysia. Most captures (20) occurred at Bukit Barisan Selatan National Park in Sumatra. Within the bay cat's region of occurrence, we deployed a total of 157 cameras in 2 landscapes for 10,023 trap nights. We detected the bay cat in the Danum Valley Conservation Area in Sabah but not in Lambir Hills National Park in Sarawak (Table A5).

3.1. Regional-scale occurrence predictors

We used GLMMs to assess relationships between number of captures and indicators of habitat degradation. We obtained count data from 97 camera-trapping surveys conducted in regions where the golden cat is known to occur, representing a total effort of 560,363 trap nights. We retained a total of 5 predictor variables to explain the observed variability in golden cat captures across all landscapes. The best predictors were forest patch size, elevation, and nearby forest cover, which all showed significant relationships with golden cat captures in univariate models ($p < 0.05$, Fig. 2.a). The most parsimonious model based on AIC model selection was a univariate quadratic model including forest patch size ($\beta = 1.82 \pm 0.72$, $p = 0.012$, $\beta^2 = -1.3 \pm 0.65$, $p = 0.045$; Table 1), closely followed ($\Delta AIC = 2.2$) by a multivariate linear model including forest patch size and forest cover ($\beta_{patch\ size} = 1.36 \pm 0.4$, $p < 0.001$, and $\beta_{forest\ cover} = 0.89 \pm 4.47$, $p = 0.058$; Table 1).

For the bay cat, we used presence and absence data from 31 camera-trapping studies in Borneo, representing a total effort of 144,370 trap nights. A univariate linear model including human population density
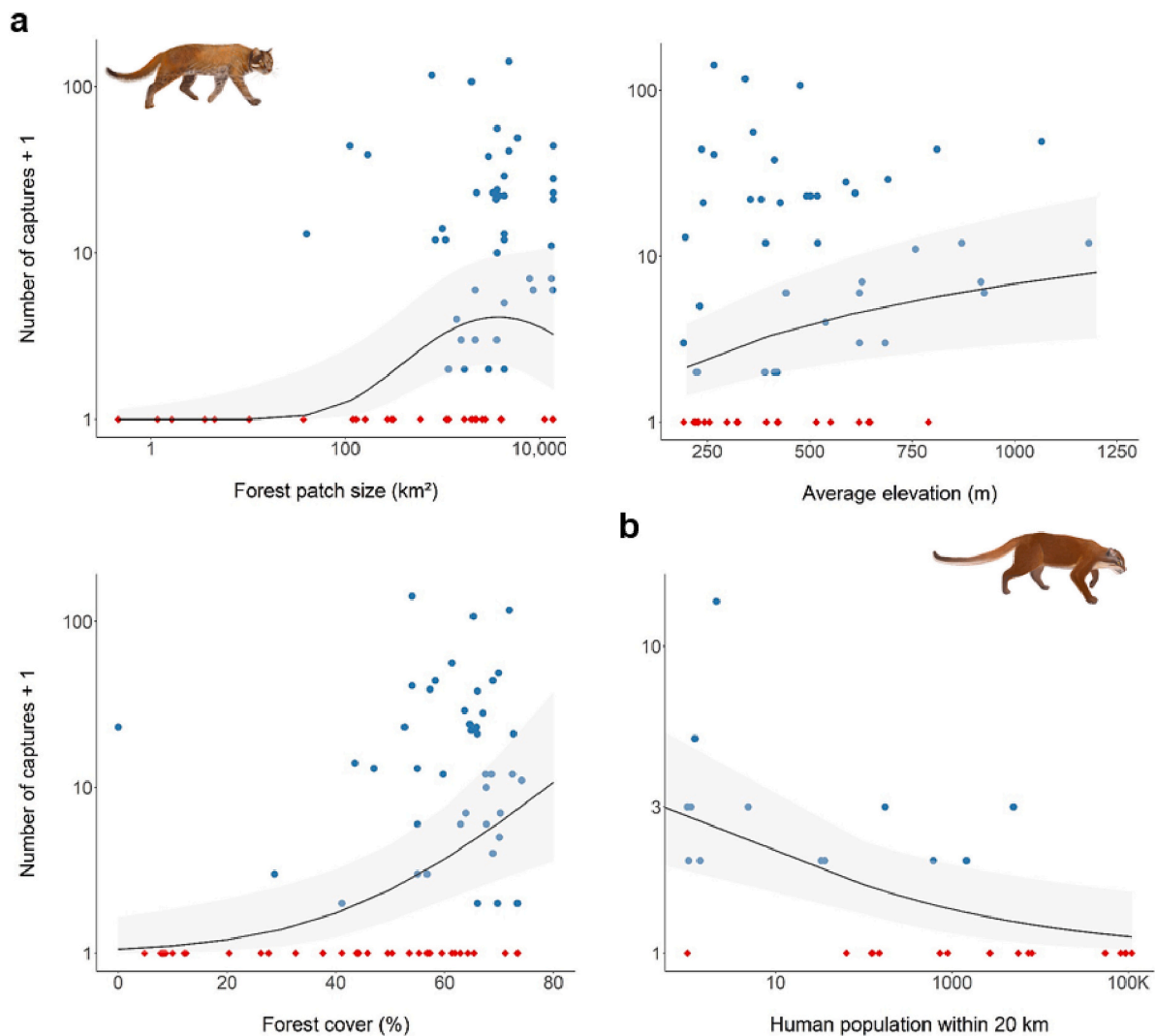
Fig. 2. Regional scale relationships between significant (*p* < 0.05) habitat predictors and number of independent captures by study for the golden cat (a) and the bay cat (b). Absences are denoted by red dots, and shaded areas represent 95 % confidence band. Relationships were modelled using GLMMs with negative binomial and Poisson distributions, respectively, and accounting for sampling effort and multiple studies from the same landscape. Details of the models are reported in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

was the only model outperforming the null-reduced model, with a significant negative effect on bay cat captures ($\beta = -9.91 \pm 0.31$, $p < 0.001$; Fig. 2.b; Table 1).

3.2. Local-scale habitat associations assessed using hierarchical occupancy modelling

The best-performing occupancy model for the golden cat included both elevation ($\beta = 3.31 \pm 1.21$; $p = 0.006$) and percentage of degraded forest ($\beta = -1.31 \pm 0.89$; $p = 0.143$). The best univariate predictors of golden cat occupancy were elevation, degraded forest, and forest loss (Table 2). Elevation had a significant positive effect, and degraded forest and forest loss both had a quasi-significant ($p < 0.09$) negative effect. Predicted occupancy was very high ($\Psi > 0.95$) above 600 m elevation, and very low ($\Psi < 0.05$) in patches with over 20 % of forest loss (Fig. 3). Contrary to McCarthy et al. (2015b), we did not find evidence of an association between golden cat occupancy and distance to river. There were insufficient captures to run hierarchical occupancy models for the bay cat.

3.3. Extent of occurrence and relative detection frequency

The area covered by the golden cat's currently recognised range in the study region, based on the species' IUCN Red List assessment published in 2015, is 215,505 km². Our own estimate based on remote-sensing forest cover data from Miettinen et al. (2016) suggests that the species' actual EOO in the region as of 2015 is 163,212 km², which represents a 24 % contraction.

The bay cat's range reported by the IUCN covers an area of 270,256 km². Our estimate of the species' EOO within that range was 236,038 km², but because 21 % of records were located outside the species' IUCN range (Fig. 5.a), we also report an enlarged estimated EOO of 353,470 km², which corresponds to the total area of remaining forest on Borneo.

While over 85 % of the golden cat's regional range falls within protected areas, <12 % of the bay cat's currently recognised range is protected (Table A2). Naïve occupancy (the proportion of landscapes with camera-trap detections compared to the total number of landscapes surveyed) for the golden cat and the bay cat was 65 % and 50 %, respectively. The mean RAI (independent detections per 100 trap nights) was over 7 times higher for the golden cat, suggesting the golden cat's relative abundance or activity is higher within occupied forests than the bay cat's (Table A2).

Table 1
GLMM performance for the golden cat and the bay cat, assessing the detection rate at the regional scale as a function of landscape habitat characteristics. Models accounted for the effect of sampling effort and multiple observations from the same landscape. Univariate non-linear models are reported only when they performed better than a linear model with the same predictor. All variables were measured within a 20-km radius area around the study centroid. Forest patch size, elevation, human population, and human footprint index were log-transformed. The univariate relationships for the best variables (golden cat: forest patch size, elevation, and forest cover; bay cat: human population) are shown in Fig. 2. Forest patch size (quadratic) refers to including Forest patch size^2 in the regression equation to test for non-linear responses (e.g. asymptotic after some threshold; $glmer(y \sim x + I(x^2))$ notation in the lme4 package in R (Bates et al., 2015).

Model	K	ΔAIC	AIC weight
C. temminckii			
~ Forest patch size (quadratic)	6	0	0.51
~ Forest patch size + Forest cover	6	2.25	0.17
~ Elevation + Precipitation	6	2.61	0.14
~ Forest patch size	5	3.49	0.09
~ Forest patch size + Elevation	6	3.58	0.09
~ Forest cover + Elevation	6	10.76	<0.01
~ Elevation	5	12.87	<0.01
~ Forest cover	5	14.06	<0.01
~ Precipitation	5	18.31	<0.01
~ Human footprint	5	19.42	<0.01
Null reduced model	4	21.7	<0.01
C. badia			
~ Human population	4	0	0.87
~ Forest cover	4	4.60	0.09
Null reduced model	3	6.13	0.04

Table 2
Hierarchical occupancy model performance for the golden cat, assessing local variation within landscapes from new camera trapping at 4 landscapes where the species was detected (out of 10 landscapes sampled). All variables were measured within a 1-km radius areas around cameras. There were insufficient bay cat captures for hierarchical occupancy modelling.

Model	K	ΔAIC	AIC weight
~ Elevation + degraded forest	8	0	0.40
~ Elevation + forest cover	8	0.21	0.37
~ Elevation	7	1.14	0.23
~ Degraded forest	7	12.36	<0.01
~ Forest loss	7	12.47	<0.01
Null reduced model	6	16.17	<0.01

3.4. Habitat suitability mapping

For MaxEnt presence-only SDMs, we obtained 53 presences for golden cats and 62 presences for the bay cat. Our MaxEnt model of habitat suitability within the golden cat's updated EOO in the study region showed significant spatial variation, ranging from isolated pockets of high habitat suitability in Peninsular Malaysia, Sumatra, northern Myanmar, Laos, and northern Cambodia, to large areas with a very low probability of presence, for the most part concentrated in Thailand, central Myanmar, and the Mondolkiri province of eastern Cambodia. In total, 9.9 % of the area within the golden cat's updated EOO had a probability of presence ≤ 0.05, and several areas even had a predicted probability of presence of zero (Fig. 4.e). The bay cat's predicted probability of presence within remaining forests across Borneo was relatively high (with a median probability of presence of 0.56) (Fig. 5.c). For both the golden cat and bay cat, the probability of presence increased with a higher percentage of forest cover and higher forest integrity (Fig. A1).

MaxEnt model performance was very high for the golden cat (mean AUC and SE for the ROC curve = 0.849 ± 0.064) and within acceptable thresholds for the bay cat (mean AUC and SE for the ROC curve = 0.675 ± 0.090).

4. Discussion

There was strong agreement among our models of regional-scale habitat associations, local-scale occupancy, and MaxEnt habitat suitability, suggesting that golden cat and bay cat conservation necessitates extensive forests with minimal anthropogenic disturbance. Considering that the region has experienced some of the world's highest deforestation rates over the past decades (Achard et al., 2002; Margono et al., 2014), and that the spatial patterns of deforestation drive much larger declines in forest integrity (Haddad et al., 2015; Grantham et al., 2020), our results suggest that both species are more threatened than previously appreciated.

4.1. Golden cat

In 2015, the IUCN Red List Cat Specialist Group estimated that the golden cat had experienced a population decline of 20–30 % over 10 years largely due to deforestation, and considered the species 'very close to qualifying for a Vulnerable status' (McCarthy et al., 2015a). Our results indicate (i) a further 24 % reduction in forested area within the golden cat's range in the study region since the last assessment; (ii) that
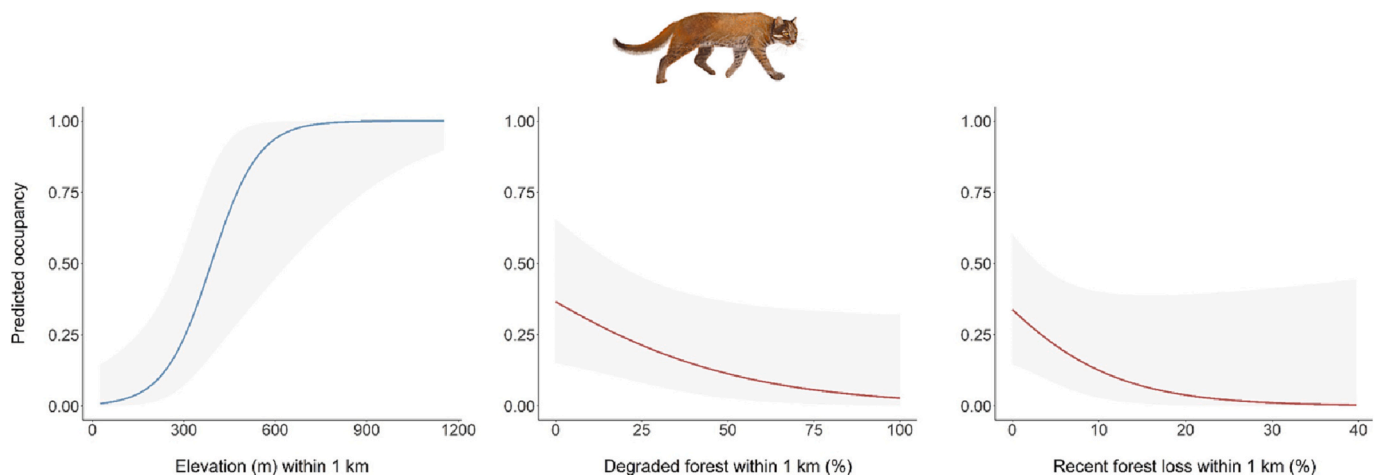
Fig. 3. Local scale (within landscapes) habitat associations for the golden cat, assessed using hierarchical occupancy modelling with detection histories from seven landscapes. Graphs show predicted occupancy relative to elevation, degraded forest, and forest loss between 2000 and 2019, measured within a 1-km radius around each camera trap station. Shaded areas represent 95 % confidence band. Details of the models are reported in Table 2.
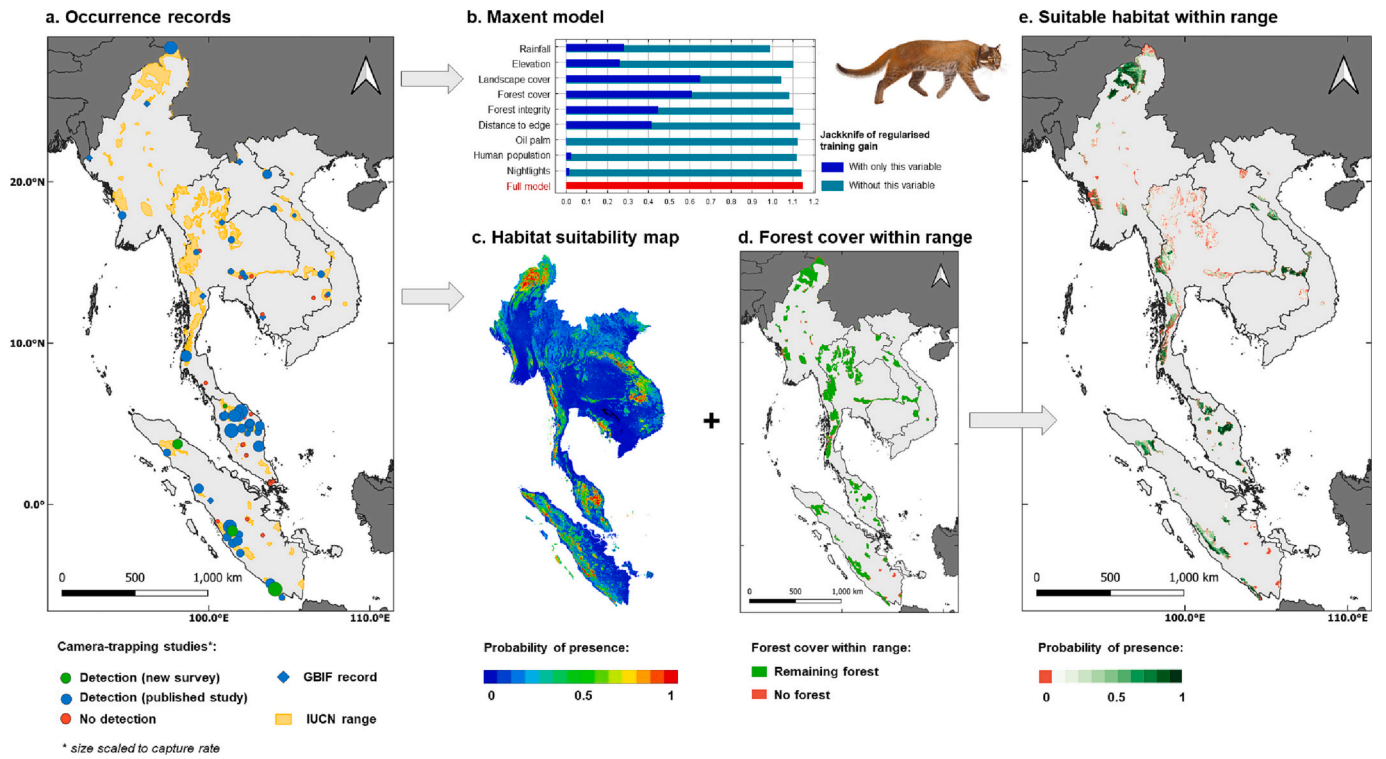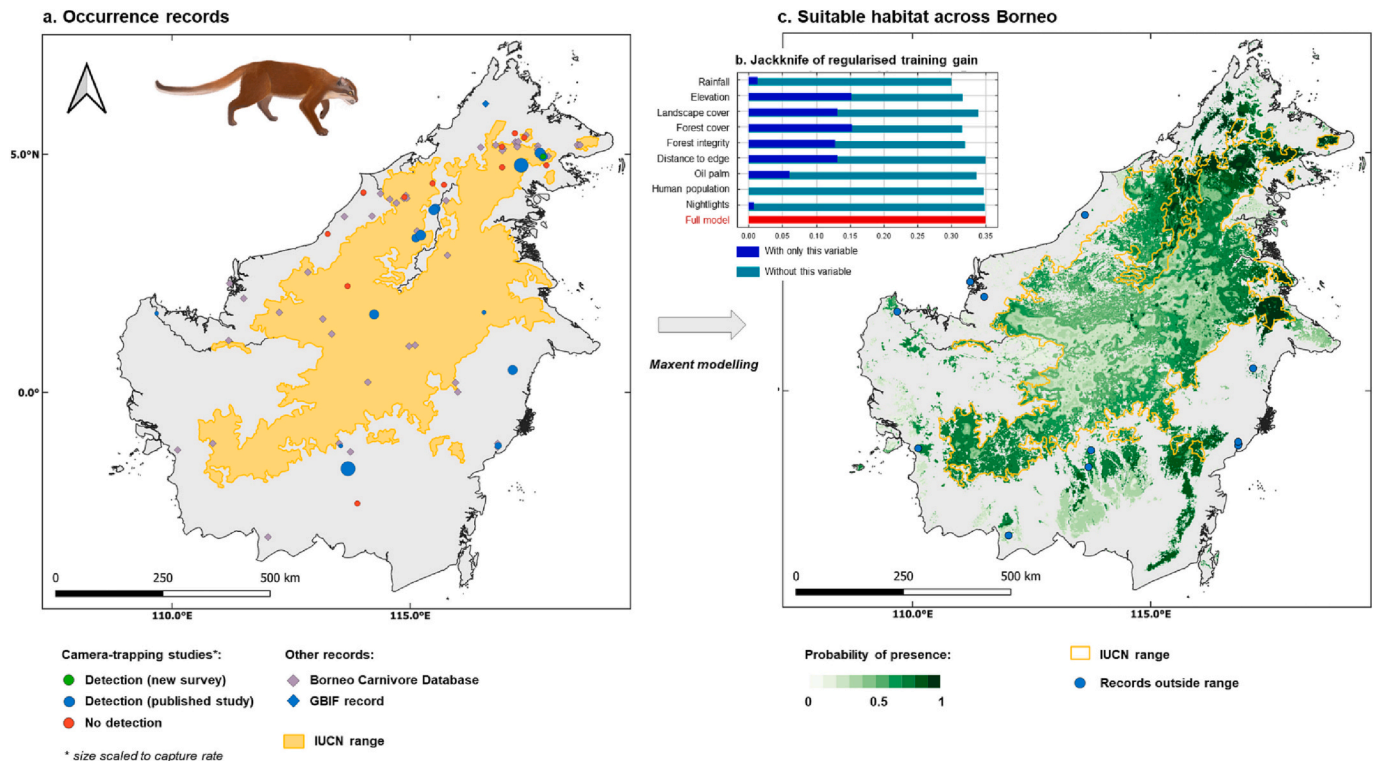
Fig. 4. Golden cat range and predicted habitat suitability in the study region: (a) IUCN range and occurrence records by data source; (b) MaxEnt model with Jackknife of regularised training gain showing variable performance; (c) habitat suitability map from MaxEnt model; (d) forest cover within IUCN range as of 2015, showing remaining forest (equivalent to EOO) and non-forested areas (assumed to be unoccupied); (e) habitat suitability map showing predicted probability of presence in remaining forest within IUCN range.

Fig. 5. Bay cat range and predicted habitat suitability in Borneo: (a) IUCN range and occurrence records by data source; (b) MaxEnt model with Jackknife of regularised training gain showing variable performance; (c) habitat suitability map showing predicted probability of presence in remaining forest across Borneo (EOO), with occurrence records outside IUCN range.

vast areas within this reduced EOO have a very low probability of presence (10 % of the total area with $p \leq 0.05$), leaving only isolated pockets of highly suitable habitat within predominantly low-suitability degraded forest; and (iii) that the species' population is becoming increasingly fragmented. The golden cat's apparent preference for higher elevation must be interpreted within the context of its wide range. For example, in Sumatra and Peninsular Malaysia, the golden cat may be under increasing threat from agricultural expansion into the region's highlands, driven by climate change (Brodie, 2016; Zeng et al., 2018). However, in Nepal or Bhutan, climate change may raise the treeline and increase habitat. Taken together, our results indicate that the golden cat faces ongoing threats from habitat loss and fragmentation.

Using the remaining forest extent as a proxy for estimating the golden cat's EOO is likely to severely overestimate the species' realised distribution and population size. Based on the golden cat's association with large, intact forests and on the substantial decline in suitable habitat within its range, there is reason to suspect a population decline and to consider a revision of the species' Red List status. Golden cats also inhabit temperate forests in Asia and although we did not investigate habitat suitability outside Southeast Asia, habitat degradation in the region alone is sufficient cause for concern. In the absence of population density estimates, we recommend that the golden cat's status be revised to Vulnerable on the basis of criterion VU A2 (in conjunction with A1c) of the IUCN Red List Categories and Criteria (i.e. a suspected population decline of >30 % over the last three generations due to a decline in extent of occurrence and/or quality of habitat) (IUCN, 2012). To confirm this suspected trend, there is an urgent need for increased data sharing and collaboration to support the development of large-scale occupancy models across the entire species' range.

4.2. Bay cat

The bay cat was associated with highland forests in areas of low human population density, with a relatively high probability of presence across most of the forested areas of Borneo. Unlike the golden cat, the bay cat's core habitat does not appear to be severely threatened by habitat fragmentation, as hill and montane primary forests in Kalimantan have remained largely intact between 2000 and 2012 (Margono et al., 2014), and the threat of oil palm expansion into these steep areas is arguably low (Pirker et al., 2016; Austin et al., 2019).

Our findings are consistent with recent habitat-modelling studies conducted by Hearn et al. (2016b); (2018), who found that the bay cat was most closely associated with areas of low fragmentation and low human footprint, with a higher probability of occurrence in core forest areas. While our MaxEnt model suggested lower suitability in the highest and steepest mountain areas of central Borneo, there is anecdotal evidence that the bay cat can be found at high altitudes (Brodie and Giordano, 2012) and our model may have been affected by sampling bias.

The bay cat was detected at much lower frequency compared to the golden cat, with a mean capture rate consistent with the detection frequency estimated by Wearn et al. (2013). This confirms that the bay cat is rare within its range, typically more so than other felids (Hearn et al., 2018; Jeffers et al., 2019). However, naïve occupancy at the landscape scale suggests that the bay cat, though rarely observed, is still present in many areas across Borneo. The finding that the bay cat is so much rarer than its *Catopuma* congener in similar habitat conditions deserves more attention (should we be concerned about inbreeding or Allee effects?).

A significant fraction of the occurrence records we gathered for the bay cat were located outside its currently recognised IUCN range, suggesting that it may be more widely distributed than previously thought. Specifically, our MaxEnt model suggests a relatively high probability of presence in the peat-swamp *kerangas* forests of Central Kalimantan, as well as in the Meratus Mountains in South Kalimantan and in the highland regions of the Berau district of East Kalimantan, where, to our

knowledge, the bay cat has never been recorded. These areas are more exposed to habitat degradation than the island's interior forests. While the bay cat has been observed in degraded forests (Kitchener et al., 2004; Wearn et al., 2013; Mathai et al., 2014; Sastramidjaja et al., 2015; Hearn et al., 2018; Mohd-Azlan et al., 2019), our results and evidence from other studies (Brodie et al., 2015; Mohd-Azlan et al., 2022) suggest a low tolerance for disturbed habitats. Recent sightings indicating that the bay cat is present in heath and peat-swamp forests (Cheyne et al., 2017; Jeffers et al., 2019) are alarming, as these biomes have suffered severe and extensive loss in forest cover and remain threatened (Margono et al., 2014; Nikonovas et al., 2020).

4.3. Future research

The aims of our paper were to assess how threatened mid-sized felids responded to dominant habitat disturbances in tropical Asia, and to do so – for the first time – using large-scale syntheses of available data. This fills a key gap between prior work focusing on apex predators like tigers and clouded leopards (e.g. Luskin et al., 2017; Haidir et al., 2020a; Amir et al., 2022a) and more site-specific work on smaller felids (Silmi et al., 2021; Hendry et al., 2023). Another key question for mid-sized felids is whether they are experiencing mesopredator release in forests where tigers, leopards and/or clouded leopards have been lost. We investigated how to properly infer species interactions from camera-trap data, ultimately leading to a methods paper on this topic (Amir et al., 2022b). The conclusion is that hierarchical co-abundance modelling is possible but requires sample sizes that were not yet achieved for either *Catopuma* species, despite a decade of fieldwork from our team.

5. Concluding observations

This study provides the most comprehensive and up-to-date account of habitat associations for the golden cat and the bay cat. With a fate bound to Southeast Asia's dwindling forests and a poor tolerance to disturbance, both species are at risk of becoming extirpated from many of the region's remaining forest fragments. To halt their probable demographic decline, conservation efforts should focus on ensuring that suitable habitat remains immune from further degradation and disturbance. The golden cat, whose range is already largely covered by existing protected areas, requires substantial and rapid improvements in protection effectiveness, starting with more stringent limitations on logging and land clearing and/or more effective enforcement of existing regulations, including against poaching. Habitat restoration efforts aiming at increasing connectivity within and between landscapes are also crucial to maintain dispersal ability and genetic diversity. For the bay cat, whose habitat remains largely unprotected, spatial prioritisation assessments should be conducted to identify high-priority areas for conservation. Both species are also likely to benefit from conservation programmes geared towards larger, endangered carnivores with similar habitat requirements, such as tigers or clouded leopards. Furthermore, considering their habitat requirements and apparent sensitivity to disturbance, the golden cat and the bay cat can be used as indicator species for ecological research and conservation planning to evaluate landscape-level habitat quality (Crooks, 2002). Crucially, in areas where apex predators have been extirpated, these charismatic felids could act as umbrella species to protect forest fragments with high biodiversity value. In the context of widespread apex predator declines, mid-sized felids are likely to play increasingly important roles, both ecologically and as conservation icons.

CRediT authorship contribution statement

Henri Decœur: Conceptualization, Formal analysis, Methodology, Writing – Original Draft, Revision; **Matthew Scott Luskin**: Conceptualization, Data collection, Data Curation, Formal analysis, Methodology, Writing; **Calebe P. Mendes** & **Zachary Amir**: Data Curation, Formal

analysis; **Jonathan H. Moore**: Data collection, Data Curation.

Declaration of competing interest

Data availability

Datasets and R code are available via the Figshare online repository at: https://doi.org/10.6084/m9.figshare.19288439.

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